# Review of Octocorallia (Cnidaria: Anthozoa) from Hawai'i and Adjacent Seamounts. Part 3: Genera *Thouarella*, *Plumarella*, *Callogorgia*, *Fanellia*, and *Parastenella*[1]

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**Abstract:** Ten species of Hawaiian primnoids are described and/or discussed, completing the review of the 28 primnoids known from the Hawaiian Islands. This family constitutes 29% of the Hawaiian octocoral fauna. *Callogorgia americana* is synonymized with *C. gilberti*, resulting in a disjunct distribution in the Pacific and Northwest Atlantic. Two new species are described (*Plumarella circumoperculum* Cairns and *Parastenella bayeri* Cairns), and two (*Callogorgia gilberti* and *C. robusta*) are reported for the first time since their original descriptions over a century ago. Keys are provided for the Hawaiian primnoid genera and all species of the genus *Parastenella;* comparative tables are provided for the Hawaiian *Callogorgia* and *Fanellia*. A distinctive nematocyst pad is described for the genus *Parastenella*. Highly modified polyps caused by copepod parasites are described for two species: *Callogorgia gilberti* and *Thouarella hilgendorfi*.

This is the third in a series of papers that describes the deepwater octocoral fauna of the Hawaiian Islands and adjacent seamounts, the first two being Cairns and Bayer (2007) and Cairns (2009*a*). The rationale for the series and a history of the Hawaiian octocoral fauna are given in part 1 (Cairns and Bayer 2007). This contribution completes the analysis of the Primnoidae from this archipelago.

## Materials and Methods

Specimens were examined from 42 stations of seven vessels, including three research submersibles, and were made from the entire length of the Hawaiian Islands at depths of 106–1,723 m (see Appendix). All specimens are deposited at the NMNH. The scanning electron microscope images were taken by me (stub numbers prefaced by C) and F. M. Bayer (stub numbers prefaced by B). Specimens should be presumed to be preserved in alcohol unless otherwise stated in the material examined sections. A "confirmed" depth range is reported for each species (i.e., the depth of the shallowest deep to the deepest shallow ranges of individual stations).

Unlike the first two parts in this series, the order Alcyonacea (see Bayer 1981) is used to include the calcaxonian octocorals, not Gorgonacea. Also, the term polyp is used in preference to calyx (see Bayer et al. 1983).

Abbreviations: *Alb*, U.S. Fish and Wildlife Service *Albatross;* BW, body wall scale; HURL, Hawai'i Undersea Research Laboratory; IL, inner lateral scale; L:W, length to maximum width of a sclerite; MNHN, Muséum National d'Historie Naturelle (Paris); NHM, The Natural History Museum, London; NMNH, National Museum of Natural History, Smithsonian (cataloged specimens prefaced with USNM [U.S. National Museum]); OL, outer lateral scale; SEM, scanning electron microscope; *TC*, *Townsend Cromwell*; ZMA, Zöologisch Museum, Amsterdam.

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## RESULTS AND DISCUSSION

As mentioned in part 2 (Cairns 2009*a*), the primnoids form a substantial part of the octocoral fauna of the Hawaiian Islands as well as meaningfully contributing to the large, habitat-forming benthic organisms in deep water. The 28 primnoid species known from the Hawaiian Islands (Table 1) constitute 29% of the 96 octocoral species known from the archipelago, as well as 11.7% of the 239 known primnoid species and 25% of the 36 primnoid genera (Cairns and Bayer 2009). The 105 Hawaiian octocoral species reported by Eldredge and Miller (1995) was an overestimation that included many unnamed species listed in Grigg and Bayer (1976), and their number of 17 endemics was certainly a gross underestimation.

Among the 28 primnoid species, most (18, or 64%) are endemic to the Hawaiian Islands, six species (21%) have a shared distribution with the western Pacific, two species (7%) share with the larger Indo-West Pacific region, and one each has extended distributions in the eastern Pacific and the North Atlantic (Table 1). As the deepwater fauna becomes better known it is anticipated that the endemic percentage will decrease and the western Pacific component will increase. For example, this happened when the deepwater Scleractinia became better known, with the endemic percentage in that order decreasing from 70% in 1943 (Vaughan and Wells 1943) to 48% (Cairns 1984) to 21% (Cairns 2006*b*). And, although the slight connection to the eastern Pacific is not unexpected, the presence of *Callogorgia gilberti* in the North Atlantic, and the great similarity of *Parastenella bayeri* to the North Atlantic *P. atlantica*, points toward a potential cosmopolitan or otherwise unexplained zoogeographic connection between these two regions. The deepest-known primnoid from the Hawaiian Islands is *Narella hawaiinensis*, found at 1,921 m, followed closely by the two species of *Candidella* at 1,801–1,802 m. The shallowest primnoids are the *Fanellia* species.

To facilitate identification of the Hawaiian primnoids, a key to the genera is provided here.

TABLE 1

The 28 Species of Primnoidae Known from the Hawaiian Islands, Including Their Extralimital Distribution and Known Depth Range

| Genus/Species | Distribution[a] and Known Depth Range |
|---|---|
| *Thouarella* (*Diplocalyptra*) | |
| *T.* (*D.*) *biserialis* (Nutting, 1908) | E: 73–426 m |
| *Thouarella* (*Euthouarella*) | |
| *T.* (*E.*) *hilgendorfi* (Studer, 1878) | IWP: 174–750 m |
| *Plumarella* | |
| *P. circumoperculum* Cairns, n. sp. | E: 432–1,373 m |
| *Callogorgia* | |
| *C. robusta* Versluys, 1906 | WP: 520–1,301 m |
| *C. formosa* Kükenthal, 1907 | IWP: 296–750 m |
| *C. gilberti* Nutting, 1908 | also NW Atlantic: 183–965 m |
| *Fanellia* | |
| *F. tuberculata* (Versluys, 1906) | WP: 128–400 m |
| *F. euthyeia* Bayer & Stefani, 1989 | E: 305–419 m |
| *F. medialis* Bayer & Stefani, 1989 | E: 395–1,028 m |
| *Narella* | |
| *N. dichotoma* (Versluys, 1906) | WP: 204–1,448 m |
| *N. bowersi* (Nutting, 1908) | EP: 1,218–2,500 m |
| *N. ornata* Bayer, 1995 | E: 748–1,007 m |
| *N. gigas* Cairns & Bayer, 2007 | E: 362–399 m |
| *N. alata* Cairns & Bayer, 2007 | E: 477–750 m |
| *N. vermifera* Cairns & Bayer, 2007 | E: 271–527 m |
| *N. macrocalyx* Cairns & Bayer, 2007 | E: 1,206–1,807 m |
| *N. muzikae* Cairns & Bayer, 2007 | E: 326–381 m |
| *N. hawaiinensis* Cairns & Bayer, 2007 | E: 1,492–1,921 m |
| *Paracalyptrophora* | |
| *P. echinata* Cairns, 2009 | E: 708–1,475 m |
| *P. hawaiinensis* Cairns, 2009 | E: 320–870 m |
| *Calyptrophora* | |
| *C. wyvillei* Wright, 1885 | WP: 784–1,278 m |
| *C. angularis* (Nutting, 1908) | E: 366–1,723 m |
| *C. clarki* Bayer, 1951 | E: 808–1,105 m |
| *C. pileata* Cairns, 2009 | WP: 227–520 m |
| *C. alpha* Cairns, 2009 | E: 1,078–1,220 m |
| *Parastenella* | |
| *P. bayeri* Cairns, n. sp. | E: 517 m |
| *Candidella* | |
| *C. gigantea* (Wright & Studer, 1889) | WP: 384–1,802 m |
| *C. helminthophora* (Nutting, 1908) | E: 417–1,801 |

[a] E, endemic to Hawaiian Islands; IWP, Indo-West Pacific; WP, West Pacific; EP, East Pacific.

KEY TO THE HAWAIIAN PRIMNOID GENERA (MODIFIED FROM CAIRNS AND BAYER 2009)

1. Marginal scales fold over polyp as a circumoperculum ..... 2
1′. Marginal scales fixed, not folding over opercular scales ..... 4

2. Colonies pinnately branched; polyps alternately biserially arranged; marginal scales not keeled ..... *Plumarella*
2′. Colonies bottlebrush or dichotomously branched; polyps in pairs, whorls, or isolated; marginal scales prominently keeled ..... 3

3. Colony bottlebrush in shape ..... *Thouarella* (*Euthouarella*)
3′. Colony dichotomously branched ..... *Thouarella* (*Diplocalyptra*)

4. Adaxial polyp surface covered with scales ..... 5
4′. Adaxial polyp surface naked or partially covered with a reduced number of smaller scales ..... 6

5. Marginal scales 4 in number ..... *Candidella*
5′. Marginal scales 8 in number, offset from opercular ..... *Parastenella*

6. Body wall scales in 2 rows ..... 7
6′. Body wall scales in 8 rows ..... 9

7. Three or 4 pairs of body wall scales ..... *Narella* (see Cairns and Bayer [2007] for key to species)
7′. Two pairs of body wall scales ..... 8

8. Body wall scales fused into rings ..... *Calyptrophora* (see Cairns [2009*a*] for key to species)
8′. Body wall scales discrete, not fused into rings ..... *Paracalyptrophora*

9. Body wall and coenenchymal scales covered with ridges, crest, or small granules ..... *Callogorgia* (see Table 2 for species distinctions)
9′. Body wall and coenenchymal scales covered with coarse tubercles ..... *Fanellia* (see Table 3 for species distinctions)

## SYSTEMATIC ACCOUNT

Subclass OCTOCORALLIA
Order ALCYONACEA
Suborder CALCAXONIA
Family PRIMNOIDAE Milne Edwards, 1857
Genus *Thouarella* Gray, 1870

DIAGNOSIS: Colonies uniplanar or bottlebrush in shape; dichotomous, pinnate, or random in branching pattern. Polyps arranged in pairs, whorls, or isolated, each protected by 6 to 8 rows of body wall scales, the 2 adaxial scale rows having smaller and fewer scales, especially near base of polyp. Marginal scales fold over operculars as a circumoperculum, the 8 scales arranged in 2 circles (inner and outer) of 4; marginals prominently keeled (often ornately) on inner surface, keels fitting into groove on outer side of their corresponding opercular scale. Operculars also arranged in 2 circles of 4, their inner surfaces usually prominently keeled, but occasionally smooth.

TYPE SPECIES: *Primnoa antarctica* Valenciennes, 1846, by monotypy.

REMARKS: Subgenus *Diplocalyptra* is characterized by having dichotomously branched colonies and marginals with well-developed distal spines; subgenus *Euthouarella* also has pointed marginal scales but colonies are pinnate to bottlebrush in branching (see Cairns and Bayer 2009:21, 34). Including *T. biserialis* in this genus (and not in *Amphilaphis*) and excluding *T. longispinosa*, as implied by Thomson and Rennet (1931:26), results in 29 species in the four subgenera of *Thouarella* s.l. (see Cairns and Bayer 2009).

DISTRIBUTION: Worldwide, 60–1,644 m (see Cairns and Bayer 2009).

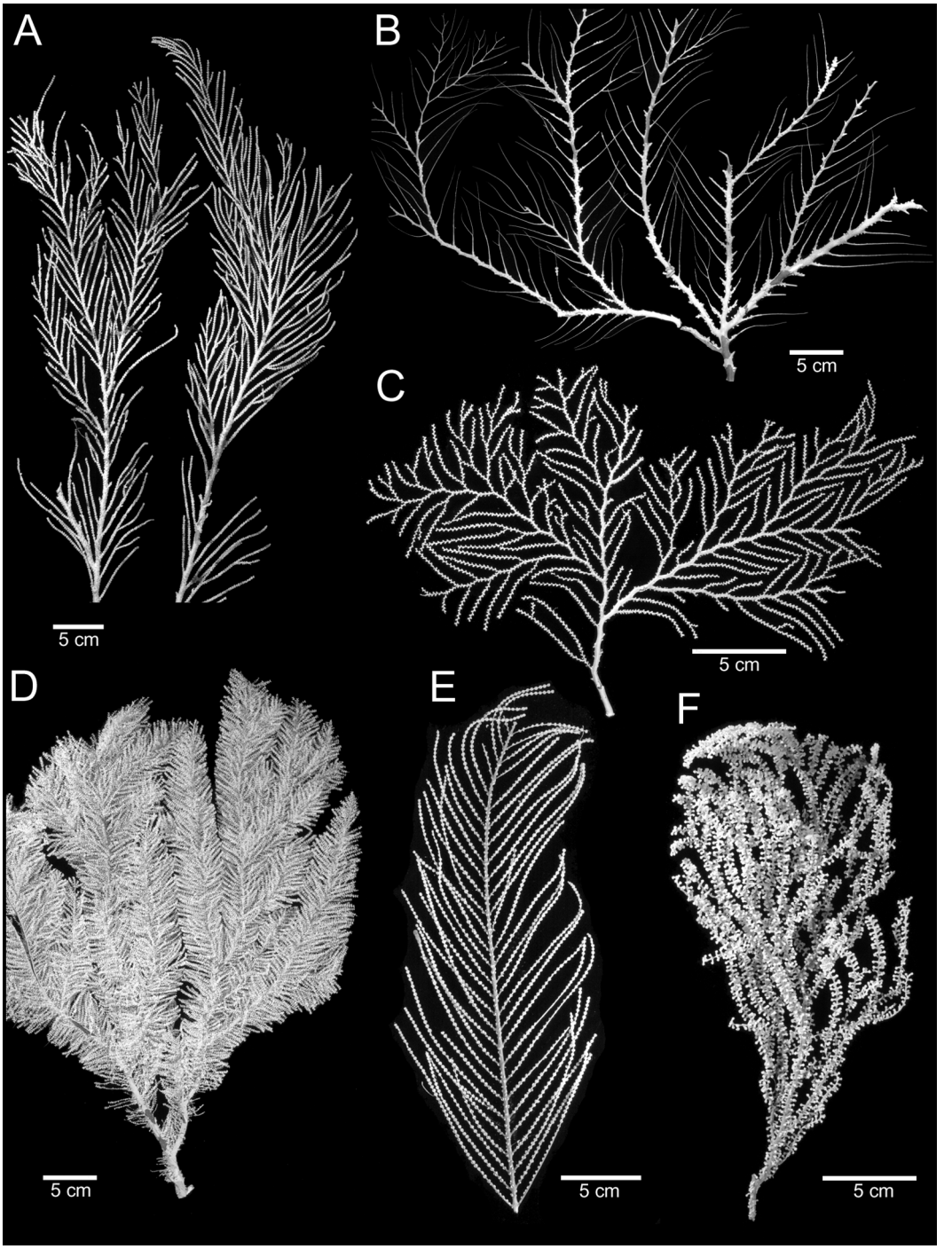


FIGURE 1. Colonial form of various species: *A*, *Callogorgia gilberti* (two branches), USNM 56813; *B*, *Callogorgia robusta*, USNM 1123725; *C*, *Plumarella circumoperculum*, n. sp., USNM 1072129 (holotype); *D*, *Thouarella hilgendorfi*, USNM 56812; *E*, *Callogorgia formosa*, USNM 60292; *F*, *Parastenella bayeri*, n. sp. USNM 1071249 (holotype).

*Thouarella* (*Diplocalyptra*) *biserialis* (Nutting, 1908)
Figures 2–3

*Amphilaphis biserialis* Nutting, 1908:573, pl. 43, fig. 4; pl. 47, fig 4.—Cairns and Bayer, 2009:28 (listed).
*Thouarella biserialis:* Kinoshita, 1908*b*:519, 520, 2 text-figs.—Kükenthal, 1915:151 (listed); 1919:438–439; 1924:301.—Parrish and Baco, 2007:192 (listed).

MATERIAL EXAMINED: The holotype.

TYPES AND TYPE LOCALITY: The holotype, consisting of two short branches (also SEM C1392), is deposited at the NMNH (USNM 22583). Type locality: 21° 56′ 25″ N, 159° 21′ 04″ W (southeast of Kaua'i), 73–426 m.

DESCRIPTION OF HOLOTYPE: The holotype, now in two fragments 4 cm and 3 cm in length, appears to be from a dichotomously branched, uniplanar colony. Polyps cylindrical, 1.2–1.5 mm in length, and curved (not straight) upward (not perpendicular to branch). Polyps occur primarily in pairs standing on opposite sides of branch in plane of flabellum, rarely in whorls of 3. Body wall scales roughly of uniform size, arranged in 8 longitudinal rows, but adaxial rows short (1–2 scales), revealing a naked adaxial face (Figure 2*E*). In polyp examined, 6–7 abaxial scales per row, 5–6 OL, 2–3 IL, and 1–2 adaxial scales. Marginal scales pointed (Figures 2*B*, 3*D*), keeled on inner surface, up to 0.4 mm in length, and having a L:W of 1.5–1.8. Marginal scales fold over smaller opercular, shielding them from view. Remaining body wall scales (Figures 2*C*, 3*C*) often wider than tall (L:W = 0.67–1.1) and up to 0.29 mm in length, those in upper polyp having a series of longitudinal ridges (Figures 2*D*, 3*C*) on distal inner surface, conferring a serrate upper edge. Opercular scales small (up to 0.28 mm in length) and bluntly tipped, with a L:W of 1.6–2.0. Outer surface granular and fairly flat; distal inner surface smooth, bearing a rounded longitudinal bulge. Coenenchymal scales elliptical, outer surface concave and smooth to slightly granular, up to 0.3 mm in diameter.

REMARKS: The basis for this species is quite scant, consisting of just one small, poorly preserved branch fragment. No additional specimens have been collected. However, based on its paucity of adaxial sclerites and dichotomous branching, it is most similar to *Thouarella* (*Diplocalyptra*) as defined by Kinoshita (1908*a*) and recently illustrated, keyed, and redefined by Cairns and Bayer (2009).

DISTRIBUTION: Known from only one specimen from the type locality.

*Thouarella* (*Euthouarella*) *hilgendorfi* (Studer, 1878)
Figures 1*D*, 4–5

*Plumarella hilgendorfi* Studer, 1878:648–649, pl. 2, figs. 15*a–e*.
*Thouarella hilgendorfi.*—?Wright and Studer, 1889:62–63, pl. 21, fig. 4.—Versluys, 1906:24–29, pl. 2, fig. 7, text-figs. 17–24.—Kinoshita, 1908*a:*21–22, pl. 5, fig. 42.—Nutting, 1912:66–67 (in part: those from Japan).—Kükenthal, 1919:415–416.—Aurivillius, 1931:248–252, pl. 5, fig. 8, text-fig. 48.—Chave and Malahoff, 1998: table 1 (listed).—Cairns, 2006*a:*188 (discussion).—Cairns and Bayer, 2009:28, fig. *6m–s* (listed).
*Thouarella typica* Kinoshita, 1907:230; 1908*a:*23–24, pl. 2, fig. 9; pl. 5, fig. 43.—Nutting, 1912:68.
Not *Thouarella hilgendorfi.*—Thomson, 1927:33–34.—Carpine and Grasshoff, 1985:32 (= *T. grasshoffi*).
*Thouarella hilgendorfi* forma *plumatilis* Aurivillius, 1931:252–256, pl. 5, fig. 9.
*Thouarella* sp. cf. *T. typica*: Grigg and Bayer, 1976:171 (listed).—Parrish and Baco, 2007:192 (listed).

MATERIAL EXAMINED: Specimen reported by Nutting (1912); *Star II* (station unknown), 21° 18′ N, 157° 32′ W (Kaiwi Channel between O'ahu and Moloka'i), 366 m, 1977, 1 large dry colony, SEM C1393–1397, USNM 56812; HURL 82-103, 1 dry branch, 1 alcohol-preserved branch, USNM 83539; *Pisces 5*-527, 2 branches, USNM 1072114; *Pisces 5*-582, 1 branch, USNM 1071228;

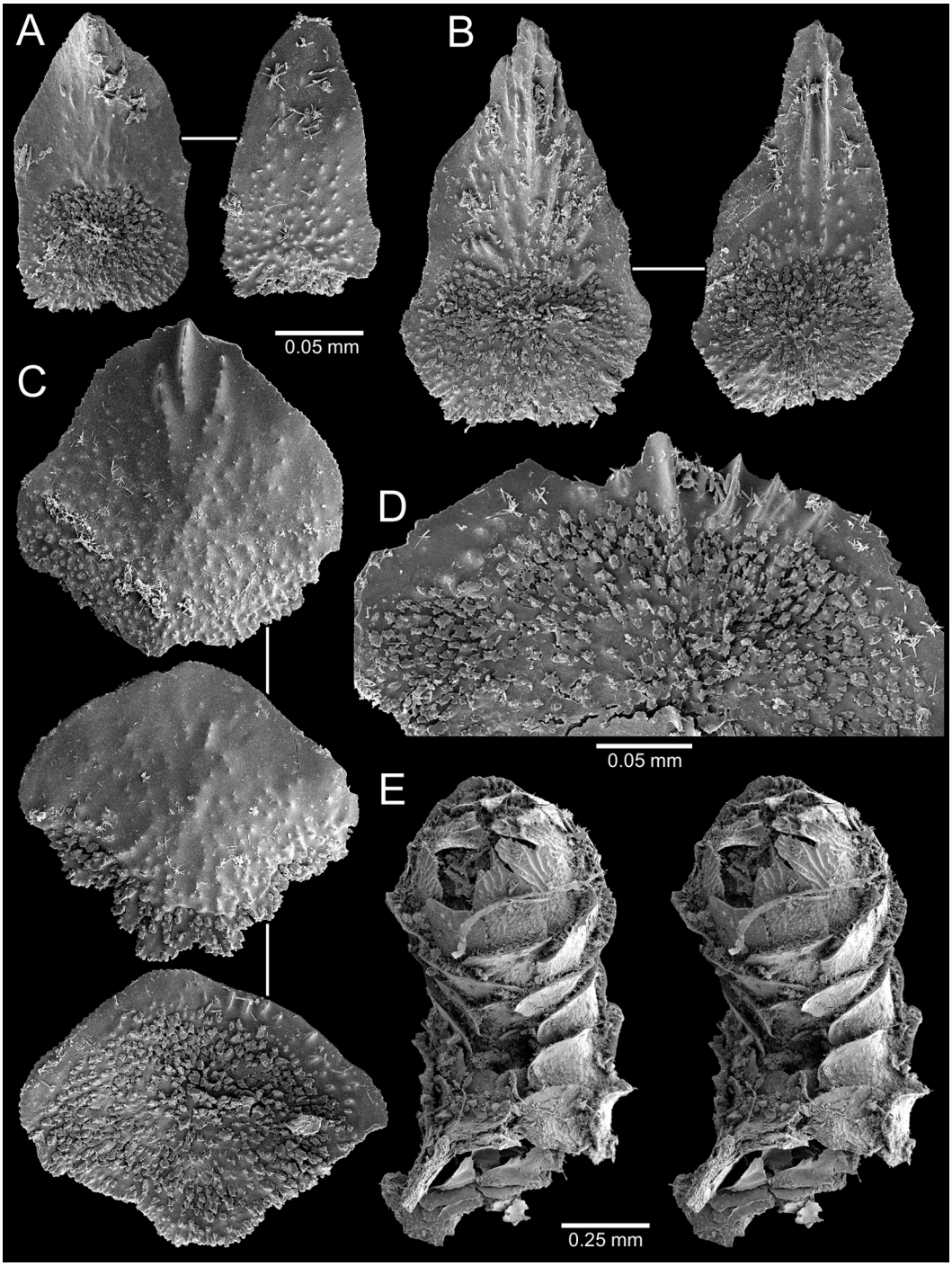


FIGURE 2. Polyp and sclerites of *Thouarella* (*D.*) *biserialis*, USNM 22583 (holotype): *A*, opercular sclerites; *B*, inner face of marginal sclerites; *C*, body wall sclerites; *D*, detail of distal inner edge of a body wall sclerite; *E*, stereo view of adaxial side of a polyp.

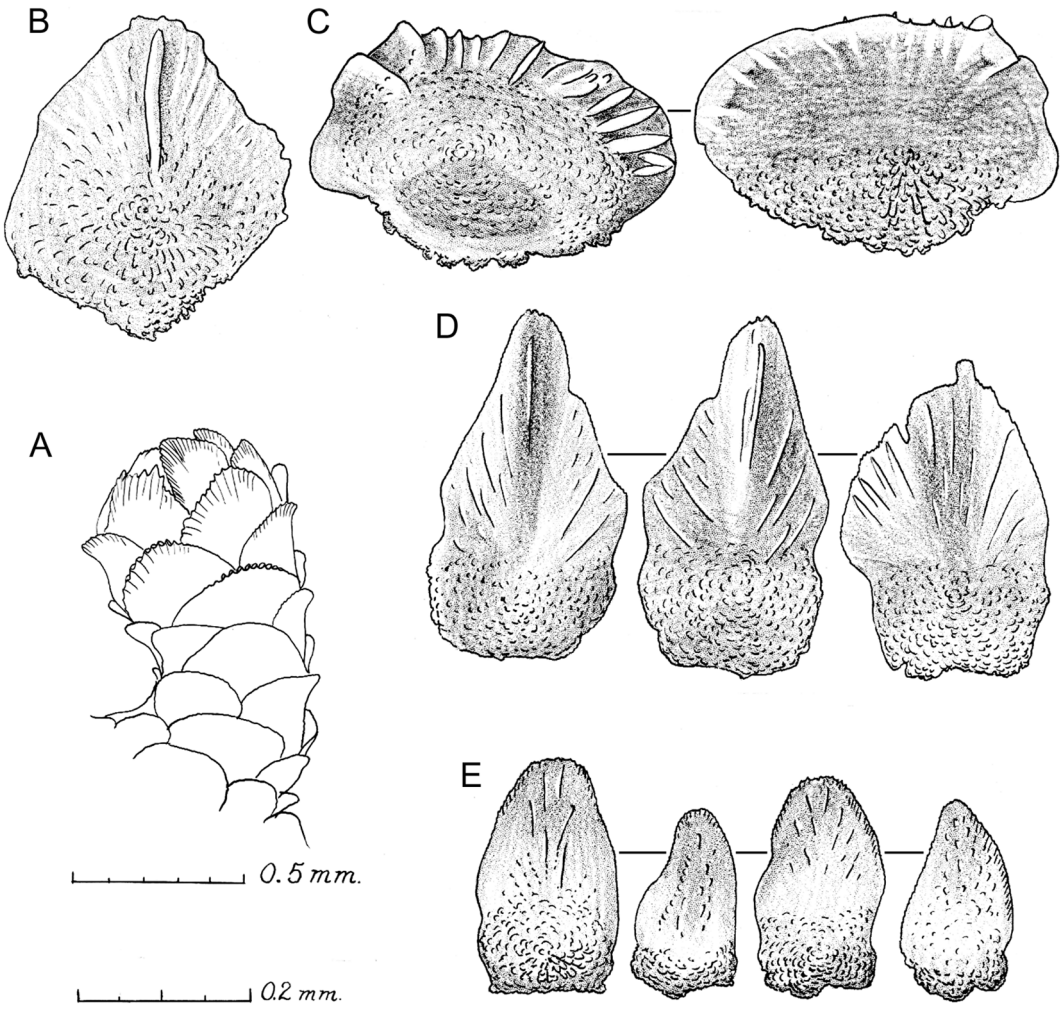


FIGURE 3. Polyp and sclerites of *Thouarella* (*D.*) *biserialis*, USNM 22583 (holotype): *A*, lateral view of a polyp; *B*, inner face of a distal body wall sclerite; *C*, abaxial body wall sclerites; *D*, three marginal sclerites; *E*, four opercular sclerites. (Figure drawn by F. M. Bayer.) Scale 0.5 mm pertains to *A;* scale 0.2 mm to *B–E.*

*Star II*-1, 1 dry colony, USNM 56811; *Star II*-2, off Makapu'u Point, O'ahu, 350–396 m, March 1978, 1 dry colony, USNM 56931 and 1092778; off Makapu'u Point, O'ahu, 366 m, date unknown, 1 branch, USNM 1114318.

TYPES AND TYPE LOCALITY: Holotype: Zoologisches Museum, Berlin, 2070 (see Versluys [1906]). Type locality: "Jeddobay" (= Tokyo Bay), Japan, 548 m.

DESCRIPTION: Colonies flabellate, consisting of several main branches that result from irregularly dichotomous branching, each main branch covered by numerous closely spaced, undivided branchlets that originate from all sides of main branches (bottlebrush arrangement), these branchlets 20–25 mm in length. Largest specimen (USNM 56812) 48 cm in height and 34 cm in width, with a broken basal stem diameter of 9.5 mm. Axis pale yellow to bronze, covered by white coenenchyme and polyps.

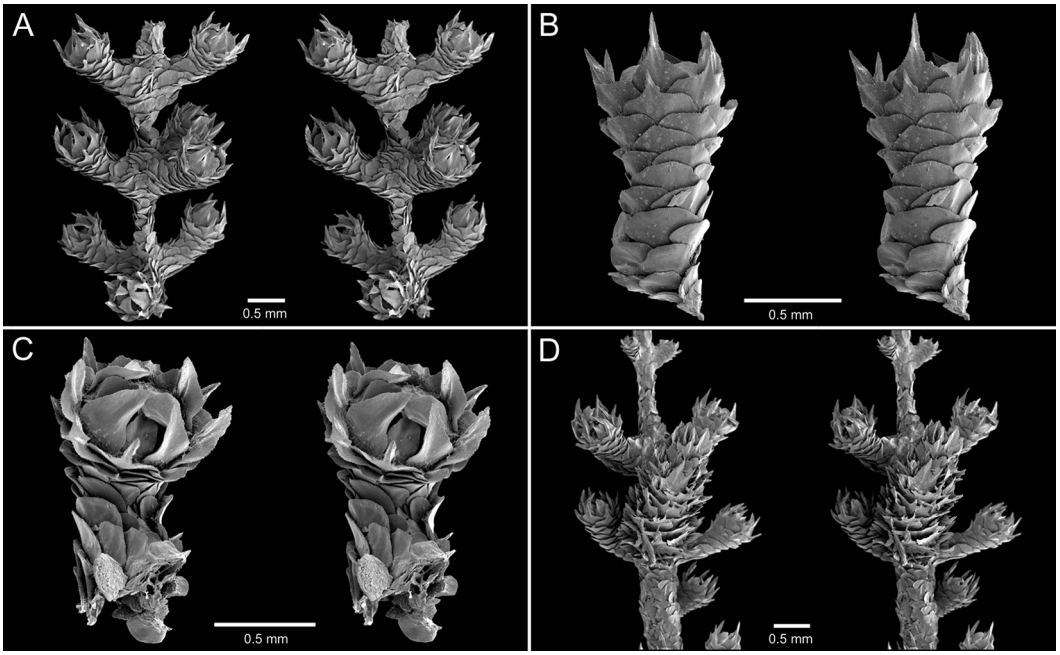


FIGURE 4. Polyps of *Thouarella hilgendorfi*, USNM 56812, stereo views: *A*, three whorls of polyps; *B*, abaxial side of a polyp; *C*, adaxial side of a polyp; *D*, whorl of polyps including one parasite-modified exemplar.

Polyps occur in pairs and in whorls of 3 on branchlets and randomly on larger-diameter branches; 6–7 whorls occur per cm; whorl diameter on distal branchlets 2.4–2.5 mm. Polyps 1.0–1.4 mm in length, flared distally, and slightly inclined upward. Approximately 1 in 20 polyps are highly modified (Figure 4*D*) by a pair of parasitic copepods, each modified polyp being much larger (up to 1.6 mm in length and 1.2 mm in diameter and thus 2–3 times volume of a typical polyp). Parasite-modified polyps lack operculars, and their body wall scales flare outward, having ridged inner faces, and a coarse serrate distal margin.

Body wall scales arranged in 8 longitudinal rows: usually 6 or 7 abaxial pairs, 5 or 6 OL pairs, 3 or 4 IL pairs, and only 1 or 2 adaxial pairs, the adaxial side of polyps covered with particularly wide adaxial and inner lateral body wall scales. Eight marginal scales broad and prominently spinose, up to 0.5–0.6 mm in height and 0.3–0.4 mm wide (L:W = 1.2–1.8), the distal 60–65% of scale occupied by the projecting spine. Outer distal surface of marginals smooth, outer proximal surface slightly granular; inner surface of spine bears 3–4 prominent, finely serrate ridges (Figure 5*D*) that fit into longitudinal furrow on outer surface of their corresponding operculars (Figure 5*C*); distal edge also finely serrate. Submarginal scales (Figure 5*E*) similar to marginals but with a much shorter distal spine (35% length of scale) and a corresponding lower L:W of about 1.2. Remaining body wall scales (Figure 5*F*) nonspinose, having a crescent-shaped, finely serrate distal margin, smooth outer surface, and are usually wider than long (L:W = 0.6–0.8). Opercular scales often arranged in 2 quartets (Figure 5*A*), alternating in size, the larger operculars 0.35–0.45 mm in length (L:W = 1.4–2.1), the smaller ones only 0.18–0.23 mm in length (L:W = 1.6–2.2) and highly curved. Outer surface of operculars smooth, with slightly serrate distal edges, and a longitudinally concave outer surface that corresponds to a smooth, convex (not ridged or keeled) inner

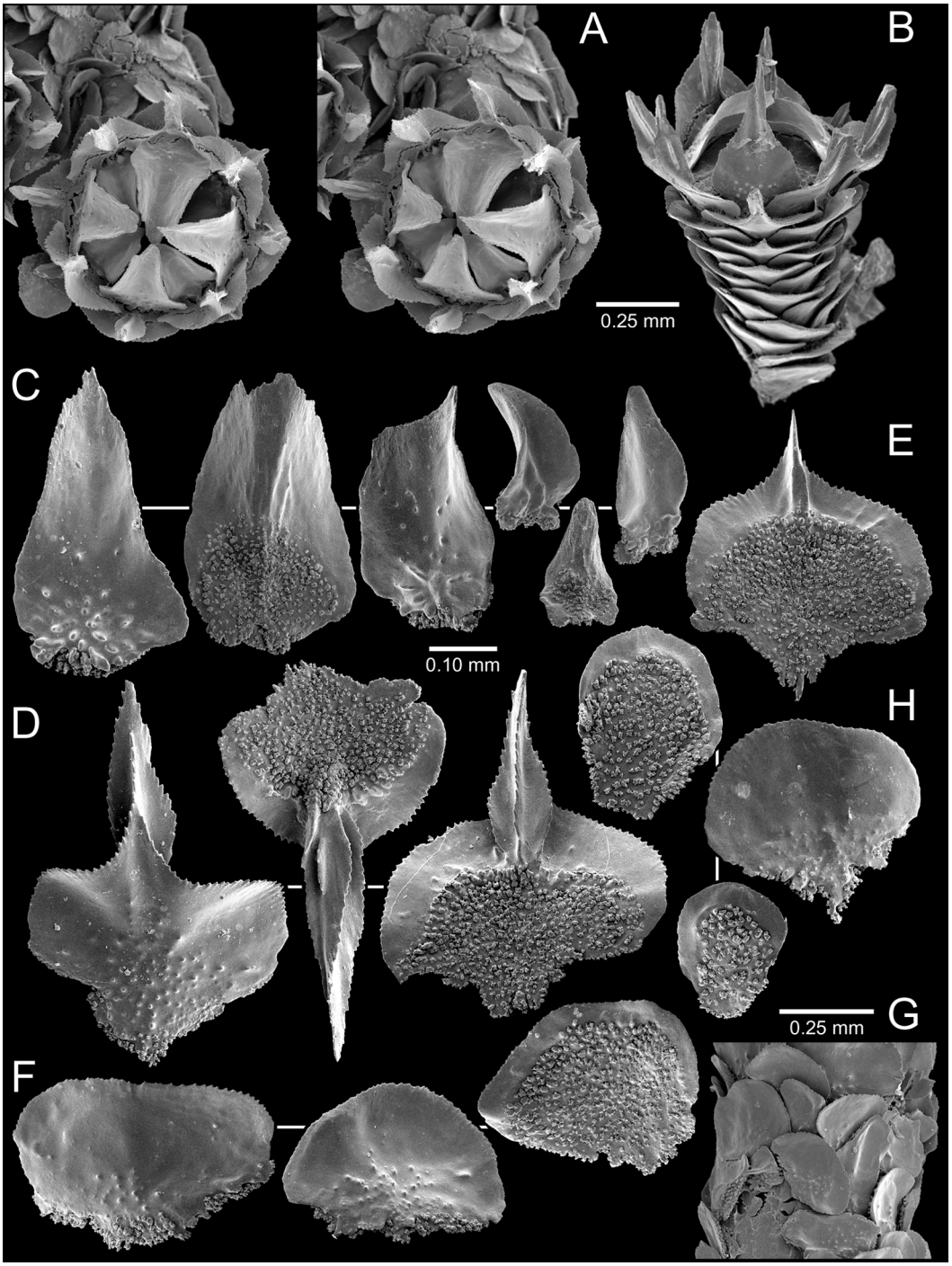


FIGURE 5. Polyps and sclerites of *Thouarella hilgendorfi*, USNM 56812: *A*, stereo opercular view showing the coordination of the 8 opercular and 8 marginal scales; *B*, oblique calicular view; *C*, opercular sclerites; *D*, marginal sclerites; *E*, inner surface of a submarginal sclerite; *F*, body wall sclerites; *G*, coenenchymal sclerites in situ; *H*, coenenchymal sclerites.

surface. Marginals also occur in 2 quartets, an inner set of 4 that correspond to the smaller operculars and an outer set of 4 corresponding to larger operculars. Likewise, submarginals occur in 2 quartets, the innermost 4 aligned with the inner marginals, and the outer 4 with the outer marginals.

Coenenchymal scales similar to body wall scales, most elliptical in shape with a smooth, flat outer surface and a finely serrate distal edge.

COMPARISONS: Cairns and Bayer (2009) listed only two other species in the subgenus *T.* (*Euthouarella*) that have a bottlebrush arrangement of polyps: *T. longispinosa* Kükenthal, 1912 (Antarctica, 385 m), and *T. grasshoffi* Cairns, 2006*a* (North Atlantic, 720–1,760 m). After an examination of the type of *T. longispinosa*, it is no longer considered to be in this genus. And, as mentioned by Cairns (2006*a*), *T. hilgendorfi*, although similar to *T. grasshoffi* in many characters, differs in having polyps usually arranged in whorls of 3 (not 2), commonly has parasite-modified polyps, lacks ridges on the inner surface of the opercular and body wall scales, has distinctive submarginals and marginals, has submarginal scales arranged in quartets, and has shorter branchlets.

This identification is based on examination of the broadly topotypic specimens from Japan (not Aleutian Islands) reported by Nutting (1912), and the excellent descriptions and figures of Studer (1878), Kinoshita (1908*a*), and Aurivillius (1931). It differs only in the common presence of parasite-induced polyps in all specimens examined, and in having slightly longer polyps.

DISTRIBUTION: Hawaiian Islands: Kaiwi Channel off O'ahu, and Pioneer Seamount, Northwestern Hawaiian Islands, 366–608 m. Elsewhere: Japan, Indonesia, Indian Ocean, 174–750 m (Kinoshita's [1908*a*] report from 2,193 m is questioned).

## Genus *Plumarella* Gray, 1870

DIAGNOSIS: Colonies uniplanar, usually pinnately branched, but may be dichotomous. Polyps usually arranged in an alternating biserial arrangement, occasionally isolated. Polyps protected by 8 rows of body wall scales, those on adaxial side sometimes smaller and fewer in number. Eight marginal scales fixed, not folding over operculum and thus usually without a keel on inner surface. Distal edge of marginal scales straight, serrate, pointed, or spinose. Inner side of opercular scales usually smooth, not keeled.

TYPE SPECIES: *Gorgonia penna* Lamarck, 1815, by subsequent designation (Wright and Studer 1889:73).

REMARKS: Twenty-one species are now known in this genus (Cairns and Bayer 2009). This is the first documented record of the genus from the Hawaiian Islands.

DISTRIBUTION: Central and western Pacific, Patagonia, northwestern Atlantic, 10–1,914 m.

*Plumarella circumoperculum* Cairns, n. sp.
Figures 1*C*, 6–7

*Amphilaphis regularis.*—Nutting, 1908:573–574.
*Plumarella* sp. Grigg and Bayer, 1976:170.—?Chave and Malahoff, 1998: table 1.—Parrish and Baco, 2007:192.
*Thouarella* (*Amphilaphis*) *regularis.*—Parrish and Baco, 2007:192.

TYPES AND TYPE LOCALITY: Holotype: *Pisces* 5-543, 1 large dry colony, 2 branches in alcohol, SEM stubs C1379–1382, 1387–1388, USNM 1072129. Paratypes: *Alb*-3973, 1 colony, USNM 25386 (= *A. regularis* of Nutting [1908]); SANGO 13-3, 1 small colony, USNM 1114317; SANGO (Midway cruise)-20, 1 colony, USNM 1114324. Type locality: 23° 14′ 24″ N, 163° 31′ 21″ W (Blank Bank, Northwestern Hawaiian Islands), 1,373 m.

DESCRIPTION: Colonies uniplanar and wider than tall; largest specimen (the holotype) 21 cm in height and 30 cm wide, with a basal branch diameter of 11 mm. Branching loosely alternate pinnate, branches slightly geniculate at points of branchlet origin; distance between branchlets on same side of a main branch 8–11 mm. Branchlets up to 37 mm in length, often producing secondary branchlets.

Polyps short (0.8–1.2 mm in length), cla-

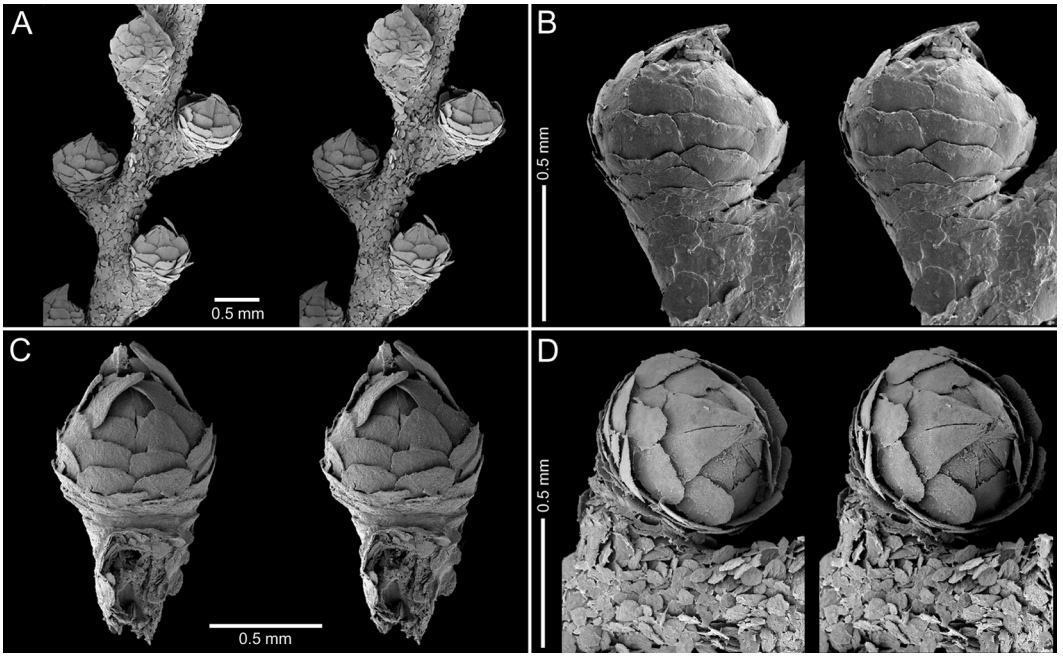


FIGURE 6. Polyps of *Plumarella circumoperculum*, n. sp. USNM 1072129 (holotype), stereo views: *A*, fragment of branch showing alternate biserial arrangement of polyps; *B*, lateral view of a polyp; *C*, adaxial view of a polyp; *D*, opercular view of a polyp showing folded circumoperculum.

vate, and vertically compressed, causing a broad overlap of body wall scales; distal polyp diameter 0.65–0.75 mm. Polyps alternate on either side of the branches and branchlets (Figure 6*A*), 9–12 occurring per cm. Polyps directed upward, with a shorter adaxial than abaxial side.

Body wall scales arranged in 8 longitudinal rows, each row having 6–8 scales, the scales becoming smaller proximally and eventually merging with coenenchymal scales in size and shape. Eight elliptical marginal scales, 0.22–0.30 mm in width, each folding over base of its corresponding opercular scale, forming a distinctive circumoperculum surrounding the operculars (Figure 6*C–D*); inner face smooth, not ridged. Submarginal scales wider than tall (rectangular) and slightly larger (0.25–0.32 mm wide) than marginals, directed upward (not inward as are the marginals), and bear a serrate distal edge (Figure 7*B*). Outer surfaces of all body wall scales, as well as operculars, smooth, having no granules or ridges. Opercular scales elongate-triangular (symmetrical), pointed, and slightly curved over top of polyp, tips of abaxial scales overreaching center of operculum (Figure 6*B–C*). Abaxial operculars up to 0.55 mm in length, with a L:W of 2.7–3.4; lateral operculars 0.44–0.39 mm in length, with a broader base and thus smaller L:W of 1.9–2.7; adaxial operculars 0.36–0.38 mm in length, with a L:W of about 2.4. Outer surface of opercular scales smooth, inner surface not ridged or keeled but smooth and somewhat longitudinally thickened.

Coenenchymal scales small (0.09–0.15 mm in diameter), elliptical, flat, and smooth (not even granules present) on outer surface with a tuberculate inner surface (Figure 7*C–D*), occurring as one layer on branches.

COMPARISONS: *Plumarella circumoperculum* has characteristics of both *Amphilaphis* and *Plumarella*, which explains why Nutting (1908) placed it in the former genus and Grigg and Bayer (1976) in the latter. The

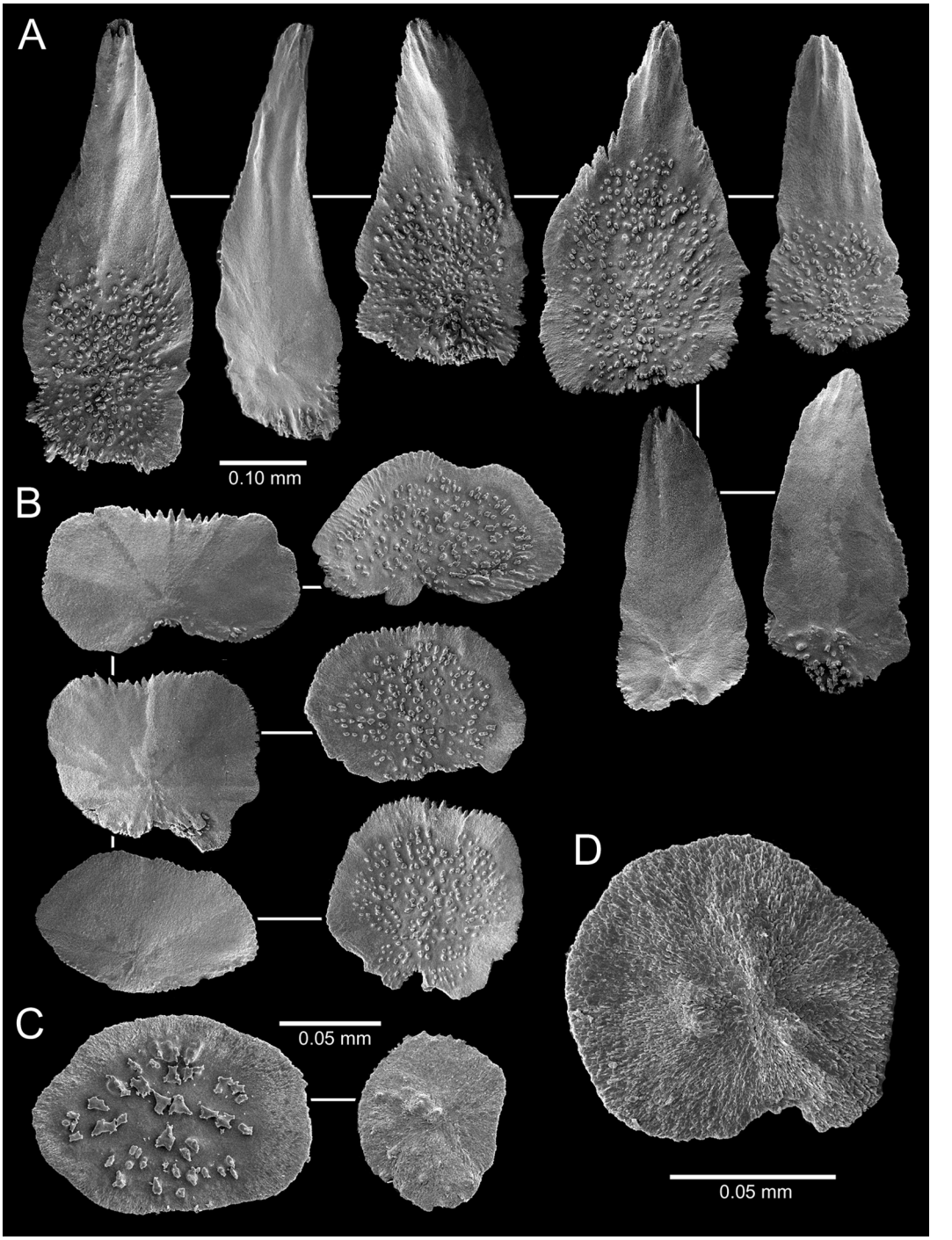


FIGURE 7. Sclerites of *Plumarella circumoperculum*, n. sp., USNM 1072129 (holotype): *A*, opercular sclerites; *B*, body wall sclerites; *C–D*, coenenchymal sclerites.

genera are quite similar, notwithstanding the facile distinction of the two in the key to the primnoid genera (Cairns and Bayer 2009). That key distinguished them based on whether the marginal scales are fixed (do not fold over the operculum), leading to *Plumarella*, or are capable of folding over the operculum as a circumoperculum, leading to *Amphilaphis*. This character is unfortunately open to interpretation in some species and specimens. Although the marginals of *P. circumoperculum* clearly form a circumoperculum, which is characteristic of *Thouarella*, several other characters are more consistent with the genus *Plumarella*, such as: the nonkeeled, nonspinose marginal scales; the nonkeeled opercular scales; and the alternate biserial arrangement of polyps. Thus, *P. circumoperculum* is tentatively placed in *Plumarella* pending a more complete evaluation of the *Plumarella-Amphilaphis-Thouarella* complex.

ETYMOLOGY: Named for its distinctive circumoperculum; the name is treated as a noun in apposition.

DISTRIBUTION: Northwestern Hawaiian Islands: Brooks Banks, French Frigate Shoals, Blank Bank, 432–1,373 m.

## Genus *Callogorgia* Gray, 1858

DIAGNOSIS: Colonies uniplanar, branchlets usually alternate pinnate in arrangement, but may also be opposite pinnate and dichotomous. Polyps arranged in whorls, the polyps facing upward. Polyps protected by 8 longitudinal rows of scales, the rows decreasing in number of scales in the abaxial to adaxial direction, such that adaxial side may be largely naked. Outer surface of body wall scales smooth, granular, or ornately ridged, the ridges sometimes continuing to inner proximal side of scale. Marginal scales fixed, not folding over opercular, the latter bearing keels or ridges on their inner surface. Coenenchymal scales elongate and usually granular.

TYPE SPECIES: *Gorgonia verticillata* Pallas, 1766, by monotypy.

REMARKS: Cairns and Bayer (2009) listed 26 species in this genus, although *C. laevis* was incorrectly included, and *C. americana* is herein synonymized. Thus the current number of species in this genus is 24. This genus has been recently discussed by Bayer (1982) and Cairns and Bayer (2002, 2009), the former including a key to the Indo-Pacific species, the latter (Cairns and Bayer 2002) a key to the Atlantic species. Kükenthal (1919, 1924) also included keys to all species up to those dates. A list of comparisons of the three Hawaiian species is provided in Table 2.

DISTRIBUTION: Indo-Pacific, North Atlantic, 37–2,472 m.

*Callogorgia robusta* Versluys, 1906
Figures 1*B*, 8–9

*Caligorgia robusta* Versluys, 1906:72–73, pl. 4, figs. 11–12, text-fig. 79.—Kükenthal, 1912:324 (listed); 1919:374–375 (keyed); 1924:273 (keyed).—van Soest, 1979:102 (type deposition).

*Callogorgia robusta*.—Bayer, 1982:122 (keyed).—Cairns and Bayer, 2009:29 (listed).

MATERIAL EXAMINED: SANGO (Midway)-17, one large dry colony now fragmented into many branches and thousands of disarticulated sclerites, SEM C1334–1338, USNM 1123725; SANGO (Midway) station unknown, 24° 03′ 35″ N, 166° 33′ 56″ W, 946–1,050 m, 1 August 1972, a branch fragment in alcohol, USNM 1114313.

TYPES AND TYPE LOCALITY: Five syntypes are deposited at the ZMA (Coel. 1827, 2285) (van Soest 1979). Type locality: *Siboga*-297: 10° 39′ S, 123° 40′ W (south of Timor, Indonesia), 520 m.

DESCRIPTION OF USNM 1123725: Colony uniplanar, and, although badly damaged, was probably about 0.5 m in height; maximum basal branch diameter 6.3 mm. Main branches dichotomous in origin and slightly geniculate at points of branchlet origin, the branchlets originating in a regular alternating pinnate arrangement, the distance between branchlets on same side of a branch 10–13 mm. Branchlets up to 9 cm in length, unbranched, and parallel to one another. Axis straw yellow, stiff, and round in cross section.

TABLE 2

Distinguishing Characteristics of the Hawaiian *Callogorgia* Species

| Character | *C. gilberti* | *C. formosa* | *C. robusta* |
|---|---|---|---|
| Colony shape; axis shape | Alternate pinnate; geniculate | Opposite pinnate; straight | Alternate pinnate; geniculate |
| Branchlets: length and further branching | 6–8 cm, occasional bifurcation | To 15 cm, no bifurcation | To 9 cm, no bifurcation |
| Internode distance on one side of branch | 9–16 mm | 7–8 mm | 10–13 mm |
| Polyp shape and length | Highly clavate, 1.2–1.5 mm | Slightly clavate, 1.7–1.8 mm | Slightly clavate, 1.6–2.0 mm |
| Polyps/Whorl | 3–7 | 3–5 | 2–4 |
| Whorls/cm | 5 | 4 | 3.5–4 |
| Sculpture on outer surface of abaxial BW scales; scale thickness | Highly ridged, overlaps to inner side; thin | Granular, smooth, low ridges, no overlap; thin | Highly ridged, no overlap; thick |
| Number of scale pairs in abaxial BW rows | 10–12 | 8–10 | 6–8 |
| Number of scale pairs in OL BW rows | 4–5 | One less than abaxial number | 1–2 |
| Number of scale pairs in IL BW rows | 2–3 | 2–4 | 1 |
| Number of scale pairs in adaxial BW rows | 1–2 | 1–2 | 1 |
| Operculum height; H:W of abaxial operculars | Low; 1.8–2.3 | Moderately tall; 1.8–1.9 | Tall; 2.5–3 |
| Other distinctive characters | Basal branches rectangular in cross section | | Abaxial marginals sometimes rostrate; OL body wall scales massive |
| Distribution | Hawai'i, 326–965 m; NW Atlantic, 183–732 m | Hawai'i, 296–472 m; Indian Ocean, 362–750 m | NWHI, 922–946 m; Indonesia, 520–1,301 m |

Polyps arranged in whorls of 3 or 4; about 3.5–4 polyps per cm; whorl diameter on distal branches 2.0–2.2 mm. Polyps also occur on main branches. Individual polyps 1.6–2.0 mm in length, slightly clavate, and usually incurved such that tip of operculum touches branch coenenchyme.

Body wall scales arranged in 8 longitudinal rows, with progressively fewer scales per row from abaxial to adaxial side, a typical polyp having 6–8 pairs of abaxial scales, 1 or 2 pairs of outer lateral scales (and occasionally 1 disjunct OL near polyp base), 1 inner lateral pair, and 1 adaxial pair (the marginals), the proximal adaxial region of the polyp being uncovered. Proximal 2 or 3 pairs of abaxial scales thick and crescent-shaped, with a smooth to granular outer surface, almost encompassing polyp base. Distalmost 2 or 3 pairs of abaxial scales (Figures 8*B*, 9*C*) bear a series of tall (up to 0.04 mm), longitudinally oriented ridges, which extend to distal edge of each scale resulting in a finely serrate edge; ridges do not overlap to inner side of scales. Distal edge of marginal abaxial body wall scales usually straight, but in some cases forms a triangular rostrum (Figures 8*B*, 9*B*). Outer lateral scales fairly wide and also longitudinally ridged on their abaxial side (Figure 9*D*), but nonetheless easily distinguished from abaxial scales. Inner lateral and adaxial body wall scales somewhat smaller, flat, and smooth to slightly granular exteriorly.

Opercular scales elongate-triangular with a flat outer surface that is prominently, longitudinally ridged and spinose (Figure 9*A*). Distal inner opercular surface bears a longitudinal mound that has 2 or 3 longitudinal, serrate ridges, not unlike those on their outer surface. Adaxial operculars up to 0.95 mm in length, having a L:W of 2.5–3.0; lateral operculars slightly smaller (0.80–0.85 mm),

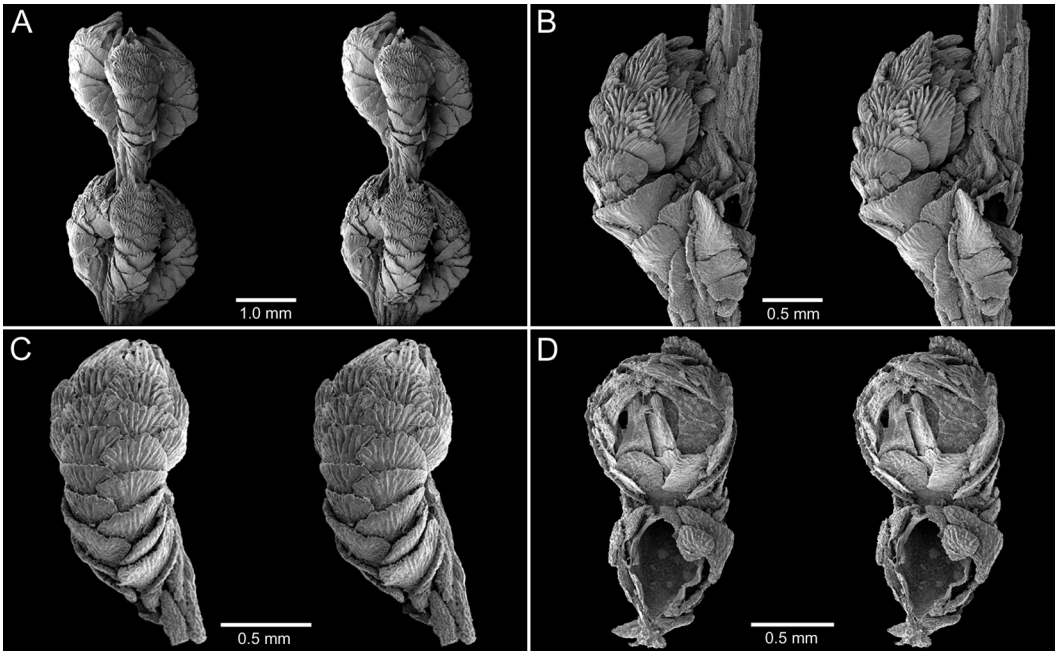


FIGURE 8. Polyps of *Callogorgia robusta*, USNM 1123725: *A*, two whorls of polyps; *B*, lateral view of a polyp showing prominently ridged body wall scales; *C*, abaxial view of a polyp; *D*, adaxial view of a polyp.

asymmetrical, with a L:W of about 2.2–2.7; adaxial operculars smallest, about 060–0.65 mm, with a L:W of 2.5–3.5. Operculum prominent and easily seen in lateral view (Figure 8).

Coenenchymal scales elongate, sometimes slightly curved or even T-shaped (Figure 9*E*), up to 1.0 mm in length, and having a L:W of up to 10. Their outer surface is granular, their inner surface tuberculate.

REMARKS AND COMPARISONS: This is the first record of *C. robusta* subsequent to its original description in 1906 and is made based on the remarkable similarity of the Hawaiian specimens to the illustrations and description of the type specimens: the Hawaiian specimens agree in every character discussed and illustrated by Versluys (1906). The Hawaiian specimens also easily key to *C. robusta* using the keys of Kükenthal (1924) and Bayer (1982). Although similar to *C. gilberti* in gross colony form, *C. robusta* differs in having larger polyps (and thus fewer per cm branch length); fewer and thicker abaxial body wall scales; and taller, ridged operculars (see Table 2).

DISTRIBUTION: Hawaiian Islands: Northwestern Hawaiian Islands off Gardiner Pinnacles and French Frigate Shoals, 922–946 m. Elsewhere: Indonesia, 520–1,301 m (Versluys 1906).

*Callogorgia formosa* Kükenthal, 1907
Figures 1*E*, 12*A*

*Caligorgia formosa* Kükenthal, 1907:208–209; 1919:366–369, text-figs. 155–159, pl. 30, fig. 1, pl. 40, fig. 47; 1924:269, text-fig. 153.—Wiktor, 1974:32.

*Primnoella indica* Kükenthal, 1907:210 (not *C. indica* Thomson & Henderson, 1906).

*Callogorgia formosa*.—Bayer, 1982:130–143, figs. 9–10.—Cairns and Bayer, 2009:29 (listed).—Parrish and Baco, 2007:191 (listed).

*Callogorgia* sp. 1 Chave and Malahoff, 1998: table 1, text-fig. 59 (in situ).

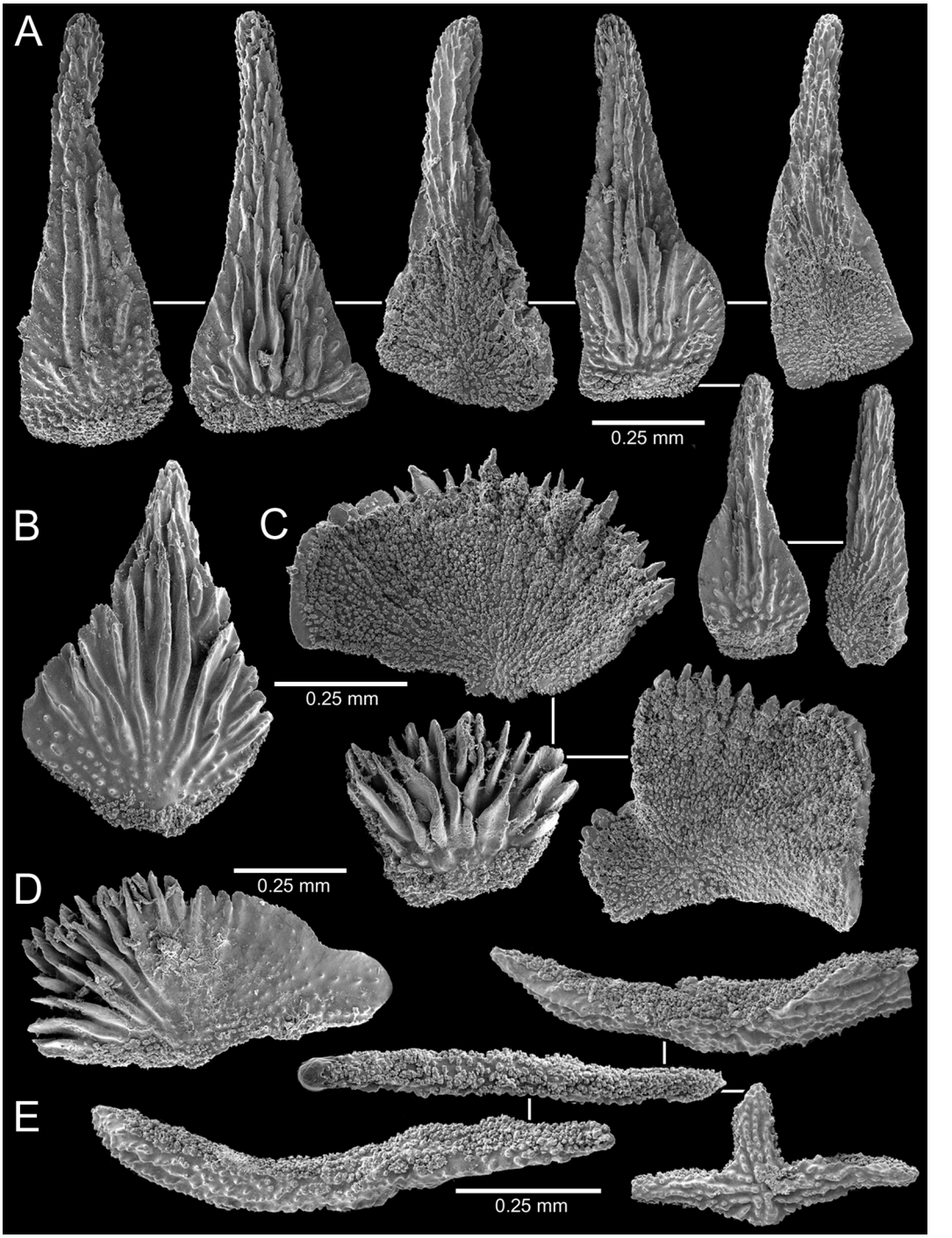


FIGURE 9. Sclerites of *Callogorgia robusta*, USNM 1123725: *A*, opercular sclerites; *B*, marginal sclerite; *C*, abaxial body wall sclerites; *D*, outer lateral body wall sclerite; *E*, coenenchymal sclerites.

MATERIAL EXAMINED: Specimens reported by Bayer (1982); HURL *Makali'i* M57, off Makapu'u Point, O'ahu, 400 m, date unknown, 3 dry branches, USNM 1092797; *Pisces 4*-45, 1 branch, USNM 1010723; *Pisces 5*-528, 1 dry branch, 1 alcohol-preserved branch, USNM 1072115; *TC* 76-06-73-15, 1 dry colony, 1 alcohol-preserved colony, USNM 78669; Chamberlain collection, off Makapu'u Point, O'ahu, 366–457 m, 1 branch, USNM 87591.

TYPES AND TYPE LOCALITY: Two syntypes are deposited at the Zoological Museum of the Wroclaw (Breslau) University (MZW 25) (Wiktor 1974). Type locality: *Valdivia*-210: southwest of Great Nicobar, Indian Ocean, 362 m.

DESCRIPTION: Colonies uniplanar and taller than wide, large colonies estimated to be up to 1 m in height. Colonies usually consist of just 1 straight (not geniculate) main branch from which pairs of branchlets diverge in a pinnate fashion on opposite sides of main branch (Figure 1*E*); distance between branchlets 7–8 mm; branchlets up to 15 cm in length, becoming shorter near branch tip. Branches stiff and pale yellow, longitudinally striate.

Polyps arranged in whorls of 3–5 (usually 4); about 4 whorls per cm; whorl diameter about 2.2 mm. Polyps also occur randomly on main branch. Polyps 1.7–1.8 mm in length, clavate, and bent over such that operculum touches coenenchyme.

Body wall scales arranged in 8 longitudinal rows, with progressively fewer scales per row from abaxial to adaxial side, the proximal adaxial side being naked (Figure 12*A*). A typical polyp has 8–10 pairs of abaxial body wall scales, usually one less pair of outer lateral scales, 2–4 pairs of inner laterals, and 1 or 2 pairs of adaxial scales. All abaxial body wall scales of about equal size, but wider than tall proximally, transitioning to taller than wide distally. Lateral and adaxial scales also of about same size; all body wall scales rather thin, with a granular base and smooth to faintly striate distal edge, their distal edges being moderately serrate, the ridges not continuing on inner side.

Opercular scales triangular and symmetrical, the adaxial operculars up to 0.4 mm tall, the abaxials 0.55 mm in height; all operculars similar in shape, having a L:W of 1.8–1.9. Outer distal face of operculars longitudinally grooved and slightly spinose, their edges serrate like body wall scales, whereas inner distal side bears a multiridged keel. Operculum easily visible in side view.

Coenenchymal scales elongate and up to 1 mm in length, having a L:W of 7–8; outer surface coarsely granular.

COMPARISONS: Among the *Callogorgia* species, *C. formosa* is unique in having opposite pinnate branching (not alternate pinnate). It is also distinctive in having numerous pairs of outer lateral body wall scales, usually just one less pair than the abaxial row.

REMARKS: This species was well illustrated by Bayer (1982), so it is not fully illustrated herein, but an adaxial view is provided (Figure 12*A*), which was missing from the other publication.

The junior synonym *Primnoella indica* Kükenthal, 1907, is also a junior secondary homonym of *C. indica* Thomson & Henderson, 1906, but its name is not replaced herein because it is considered to be a junior synonym.

DISTRIBUTION: Hawaiian Islands: Northwestern Hawaiian Islands, off Pioneer Seamount and Necker Island; off O'ahu and Maui, 296–472 m. Elsewhere: also known from off Great Nicobar Island, Indian Ocean, 362–750 m.

*Callogorgia gilberti* Nutting, 1908
Figures 1*A*, 10–11

*Caligorgia gilberti* Nutting, 1908:574, pl. 43, fig. 4; pl. 47, fig. 6.—Kükenthal, 1919:383–384; 1924:279.

*Callogorgia gilberti*.—Grigg and Bayer, 1976:170 (listed).—Chave and Malahoff, 1998: table 1, fig. 34.—Cairns and Bayer, 2009:29 (listed).—Parrish and Baco, 2007:191 (listed).

*Callogorgia americana* Cairns & Bayer, 2002:845–856, figs. 1*A–B*, 2–6. New synonymy.

MATERIAL EXAMINED: Types of *C. gilberti* and *C. americana*; *Pisces 5*-582, 1 branch,

USNM 1071239; *Pisces 5*-583, 2 branches, USNM 1071229 and 1071242; *Pisces 5*-587, branches, USNM 1071244; *Pisces 5*-589, 1 dry and 1 branch in alcohol, USNM 1071427 and USNM 1071231, respectively; *Pisces 5*-590, 1 dry branch, USNM 1071424; *Pisces 5*-668, branches, USNM 1113910; *Pisces 5*-670, dry colony, USNM 1113871; SANGO 3-1a, branches, SEM B508, USNM 59276; SANGO 3-1b, many dry branches, USNM 1123724; SANGO 3-2, 1 dry branch, USNM 1123722; SANGO 3-8, branches, USNM 1114309; SANGO 4-1, branches, USNM 1114310; SANGO 4-8, branches, USNM 1114256; SANGO 9-2, dry branches, USNM 1016672; SANGO 10-2, branches, USNM 1114254; SANGO 14-1, dry branches, USNM 1123723; SANGO 14-2, branches, USNM 1114257; SANGO Midway-25, branches, USNM 1114311; *TC* 35-23, branches, USNM 1114316; *TC* 59-20, branches, SEM B357, USNM 56787; *Star II*-1, 2 large dry branches and alcohol-preserved branches, SEM B364, USNM 56813.

TYPES AND TYPE LOCALITY: Holotype: *Alb*-4130, one colony in many parts, SEM B351, C1369–1371, USNM 25364 and one fragment at the NHM (1920.2.27.3). Paratypes: *Alb*-4130, 2 jars with many branches, USNM 25388; *Alb*-3992, 1 colony, USNM 25363; *Alb*-4041, a dead branch covered with zoanthids, USNM 25389; *Alb*-4132, 1 small branch, USNM 22592; *Alb*-4134, branches (one of them decalcified), USNM 25362, 91893, 91894. Type locality: 21° 58′ 15″ N, 159° 20′ 55″ W (east of Kaua'i), 517–565 m.

DESCRIPTION: Colonies uniplanar and taller than wide, the largest specimen known (USNM 56813) 60 cm tall and 15 cm wide, but broken basal branches 19 by 11 mm in diameter suggest a maximum height of 1–1.5 m. The relatively few main branches are dichotomous in origin and slightly geniculate at points of branchlet origin; the predominant branchlets originate in a regular alternate pinnate arrangement (Figure 1*A*), the distance between branchlets on same side of a main branch about 16 mm in lower part of

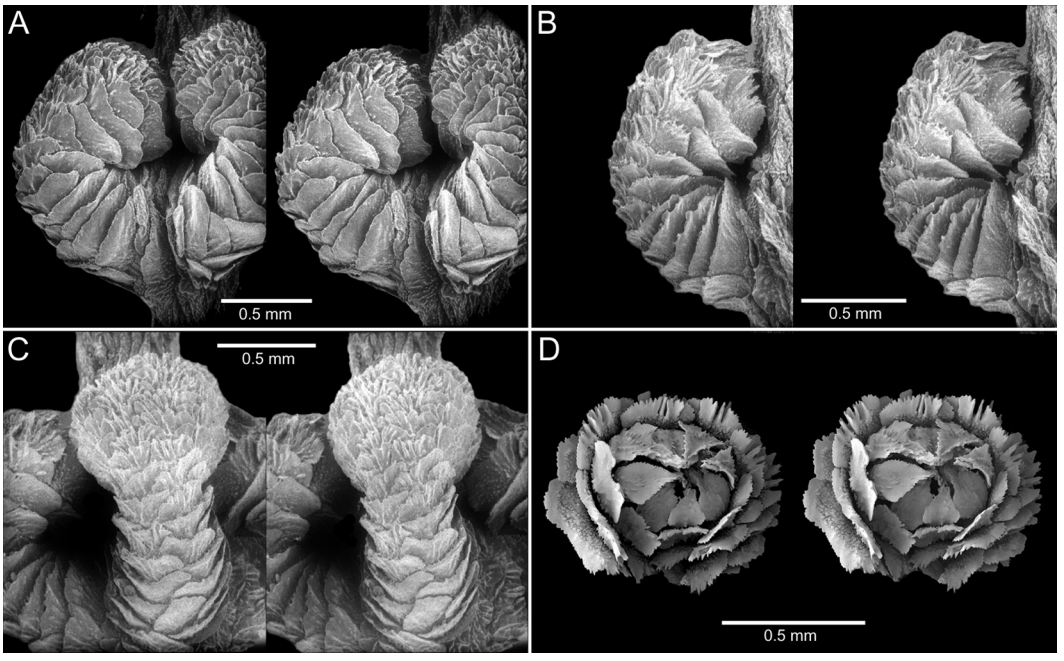


FIGURE 10. Polyps of *Callogorgia gilberti* (*A*, USNM 59276; *B–D*, USNM 25364 [holotype]), stereo views: *A*, lateral view of a polyp in a whorl; *B*, lateral view of a polyp; *C*, abaxial view of a polyp; *D*, opercular view of a polyp.

colony, decreasing to 9–10 mm in upper part. Branchlets 6–8 cm long, usually unbranched and thus parallel to one another but occasionally bifurcate. Axis yellow to brown, longitudinally striate, stiff, and circular in cross section distally but rectangular in cross section basally, the longer axis of the rectangular cross section oriented perpendicular to plane of flabellum.

Polyps arranged in whorls of 3–7, 5 being the most common complement; about 5 whorls per cm; whorl diameter on distal branchlets 1.6–2.1 mm. Polyps also occur randomly on main branches. Individual polyps 1.2–1.5 mm in length, clavate (with a pronounced clubbed end and a slim middle section), and often U-shaped in preservation, the opercular end incurved to face branch coenenchyme.

Body wall scales arranged in 8 longitudinal rows, but with progressively fewer scales per row from abaxial to adaxial side, a typical polyp having 10–12 pairs of abaxial scales, 4 or 5 pairs of outer laterals, 2 or 3 pairs of inner laterals, and 1 or 2 pairs of adaxial scales, the lower part of adaxial side being bare and closely adjacent to branchlet surface. Proximal 5 or 6 pairs of abaxial scales wide, thick, and crescent-shaped, with a smooth outer surface, each pair almost encompassing the polyp. Distal 5 or 6 abaxial pairs much thinner and narrower, bearing tall (up to 0.08 mm), longitudinally arranged ridges (i.e., cristate) (Figure 11*B*), some of which overlap to inner side of scales. Slightly distal to the origin of these reduced abaxials are the relatively wide outer lateral scales, also longitudinally ridged on their abaxial region, but smooth on their adaxial side, making a distinction between the abaxial and outer laterals difficult to distinguish. Near tip of polyps are 1 or 2 pairs of quite wide, smooth inner laterals, and adaxially there are only 1 or 2 pairs of small adaxial scales. The wide inner and outer laterals confer the widened clavate aspect to the polyps. Distal edges of scales finely serrate (i.e., ctenate to digitate) (Figure 11*B*). Several pairs of disjunct outer lateral scales may also occur near polyp base.

Opercular scales triangular, having a medially furrowed and spinose outer surface corresponding to a prominently keeled inner surface, the keel being serrate and sometimes multiple per scale. Abaxial operculars symmetrical, up to 0.39 mm in length, having a L:W of about 2.3. Lateral operculars smaller (about 0.30 mm), slightly asymmetrical, with a L:W of about 1.8. Adaxial operculars of similar size, symmetrical, with a L:W of 2.0. The operculum often lies rather flat and close to branch surface, thus not easily seen in lateral view (Figure 10*A*).

Coenenchymal scales on branchlets elongate, up to 0.7 mm in length, having a L:W of 6–8 (Figure 11*C*). Those on larger-diameter basal branches much shorter (usually less than 0.15 mm), as though degenerated from their longer state, and having the shape of those scales that constitute the modified body wall scales described in remarks for this species for crustacean-modified polyps (Figure 11*E*). Coenenchymal scales on distal branches occur in one layer; those on proximal branches are multilayered.

COMPARISONS: In a routine comparison of the Hawaiian *Callogorgia* with all other species described in the genus, it was noted that *C. gilberti* was morphologically indistinguishable from *C. americana* Cairns & Bayer, 2002, agreeing in all characters analyzed, notwithstanding the fact that *C. americana* represents a disjunct distribution encompassing the tropical northwestern Atlantic.

Neither Kükenthal (1919, 1924) nor Bayer (1982) included *C. gilberti* in their keys to the species in this genus, the former because of Nutting's incomplete original description. This is the first documented subsequent report of the species from the Pacific, which allows for a much better delineation. Of the valid species in the genus (Cairns and Bayer 2009), *C. gilberti* clearly belongs to the group of species (Bayer 1982) within *Callogorgia* that have cristate external body wall sculpture and according to Bayer's key would key closest to *C. pennacea* Versluys, 1906 (Indian Ocean, 275 m).

REMARKS: Two colonies (USNM 56813 and 1114310) show polyps modified by parasitic copepods of the genus *Lamipinna* (V. N. Ivanenko, 2009, pers. comm.). One male and one female copepod were present in each

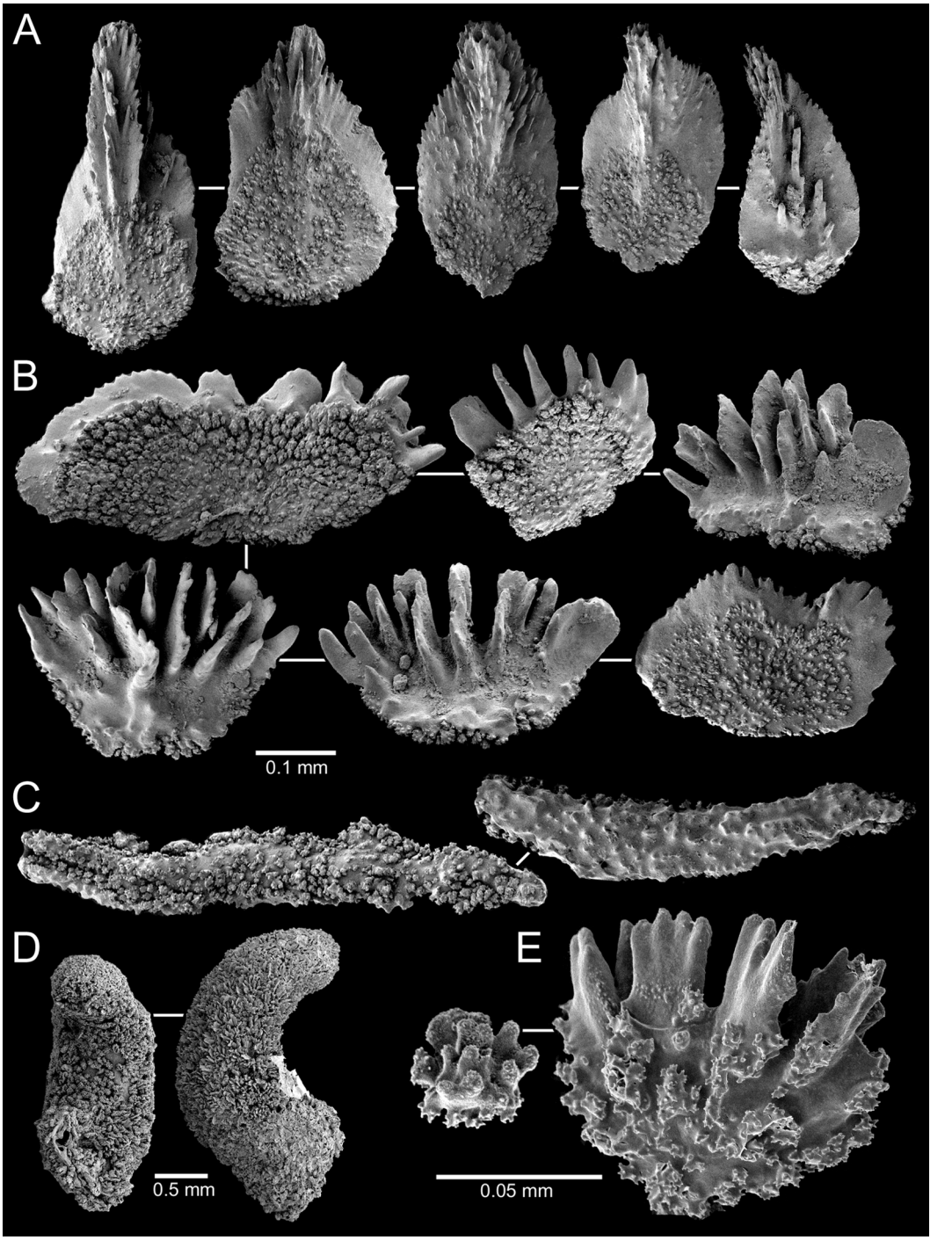


FIGURE 11. Sclerites of *Callogorgia gilberti* (*A–C*, USNM 25364 [holotype]; *D–E*, USNM 56813): *A*, opercular sclerites; *B*, prominently ridged body wall sclerites; *C*, coenenchymal sclerites; *D*, copepod-modified polyps; *E*, body wall sclerites from a copepod-modified polyp.

TABLE 3

Distinguishing Characteristics of the Hawaiian *Fanellia*

| Characters | *F. euthyeia* | *F. medialis* | *F. tuberculata* |
|---|---|---|---|
| Colony shape | Equal dichotomous | Pinnate | Loose pinnate |
| Branchlet length | 3–9 cm | 5.5 cm | <4 cm, last cm without polyps |
| Polyp length | 1.1–1.2 mm | 1.5 mm | 0.9–1.1 mm |
| Polyps/whorl at branch tip | 3 | Paired | 2–3 |
| Whorls/cm | 5–6 | 4–5 | 6–8 |
| Scale pairs in abaxial rows | 8–9 | 8–10 | 4–8 |
| Scale pairs in OL rows | 4–5 | 8–9 | 1–2 |
| Scale pairs in IL rows | 2 | 2–4 | 0–1 |
| Tip of abaxial marginals | Not pointed | Pointed | Not pointed |
| Tip of opercular scales | 1 point | Often with 2–3 points | 1 point |
| Coenenchymal bosses | Absent | Present | Absent |

polyp, but no copepodites or nauplii were found. These hypertrophied polyps are several times the size of normal individuals, and the arrangement of body wall scales is completely obliterated (Figure 11*D*). Sclerites are reduced to small (80–150 μm width), multicrested plates having serrate upper edges and a tuberculate base (Figure 11*E*, *right*), and small (45–150 μm in diameter), irregularly shaped spheroids bearing tall, blunt granules (Figure 11*E*, *left*), all of which are irregularly packed in the body wall. Opercular scales appear to be missing.

DISTRIBUTION: Hawaiian Islands: from Blank Bank to Hawai'i, and Cross Seamount; 326–965 m. Elsewhere: Northwest Atlantic, 183–732 m (see Cairns and Bayer 2002).

## Genus *Fanellia* Gray, 1870

DIAGNOSIS: Colonies usually uniplanar, branchlets arranged dichotomously or in pinnate fashion. Polyps arranged in pairs or whorls, the polyps facing upward. Polyps protected by 4–8 rows of thick body wall scales, in some cases the adaxial and IL scales being absent below the marginals. Outer surface of body wall scales covered with prominent tubercles, often arranged in ridges. Marginal scales do not fold over opercular, the latter bearing a longitudinal keel or set of ridges on inner surface. Coenenchymal scales consist of an inner layer of tuberculate spheroids covered by thick polygonal scales.

TYPE SPECIES: *Primnoa compressa* Verrill, 1865, by monotypy.

REMARKS: The three Hawaiian species in this genus were relatively recently described (Bayer and Stefani 1989) or redescribed (Bayer 1982) and well illustrated using SEM images, and thus are not redescribed here. The eight species known in the genus were keyed by Bayer and Stefani (1989). Recent works discussing species in this genus include Bayer (1982), Bayer and Stefani (1989), and Cairns and Bayer (2009). The three Hawaiian species are compared in Table 3.

DISTRIBUTION: Western and central Pacific from New Caledonia to Alaska, 92–1,028 m.

### *Fanellia tuberculata* (Versluys, 1906)

*Caligorgia tuberculata* Versluys, 1906:80–81, text-figs. 95–96; pl. 6, fig. 15.—van Soest, 1979:103 (type deposition).

*Caligorgia aspera* Kinoshita, 1908*a*:39, pl. 2, figs. 15–16; pl. 6, fig. 47.

*Caligorgia pseudoflabellum* Bayer, 1949:207, pl. 4, fig. 2, text-figs. 2*a–c*.

*Callogorgia* sp. cf. *C. tuberculata*: Grigg and Bayer, 1976:170 (listed).

*Fanellia tuberculata*.—Bayer, 1982:144–154, figs. 18–26 (full synonymy and key to species).—Bayer and Stefani, 1989:471 (keyed).—Parrish and Baco, 2007:192 (listed).

MATERIAL EXAMINED: Hawaiian specimens reported by Bayer (1982); HURL *Makali'i* M57, off Makapu'u Point, O'ahu, 400

m, small dry colony, USNM 1092796; *Star II*-1, many large dry colonies and 1 alcohol-preserved branch, USNM 56810 and 94505; *Star II*-2, 1 branch, USNM 56823; *TC* 78-5, 1 large dry colony, USNM 1123729.

TYPES AND TYPE LOCALITY: Holotype deposited at the ZMA (Coel. 2286). Type locality: *Siboga*-95: 5° 43′ N, 119° 40′ E (Sulu Sea), 522 m.

REMARKS: These four records do not appreciably add to the previously known distribution of the species. Table 3 serves to distinguish this species from congenerics in the Hawaiian Islands. In this regard it is distinctive in having a loose, pinnate branching mode and in lacking polyps on the last cm of its branchlets.

DISTRIBUTION: Hawaiian Islands: Middle Bank and off O'ahu, 362–400 m. Elsewhere: Sulu Sea, Bikini, Japan, 128–522 m.

*Fanellia euthyeia* Bayer & Stefani, 1989

*Fanellia euthyeia* Bayer & Stefani, 1989:474–475, pls. 39–40, 41*a–d*.—Cairns and Bayer, 2009:30 (listed).—Parrish and Baco, 2007:192 (listed).

MATERIAL EXAMINED: Types; *Pisces 5*-535 (specimen 6), large dry colony and some alcohol-preserved branches, USNM 1072120; *Star II*-2, a large dry colony, USNM 56823; 1 large dry colony from type locality (*TC* 76-06-73-15), USNM 1123727.

TYPES AND TYPE LOCALITY: Holotype deposited at the NMNH (USNM 79967); a paratype also at the MNHN (Oct. 1987.22). Type locality: 23° 33′ N, 164° 54′ W (near Necker Island), 419 m.

REMARKS: These three records are the first subsequent to the original description and extend the known distribution substantially both to the east and west of the type locality. Table 3 serves to distinguish this species from congenerics in the Hawaiian Islands. *Fanellia euthyeia* is distinctive in having an equal, dichotomous growth form.

DISTRIBUTION: Northwestern Hawaiian Islands, off Raita Bank and Necker Island, also off Moloka'i, 305–419 m.

*Fanellia medialis* Bayer & Stefani, 1989

*Fanellia medialis* Bayer & Stefani, 1989:473–474, pls. 37–38, 42.—Cairns and Bayer, 2009:30 (listed).—Parrish and Baco, 2007:192 (listed).

MATERIAL EXAMINED: Types; *Pisces 5*-582, 1 colony, USNM 1071240; SANGO 3-7, 1 colony, USNM 1112695; SANGO 14-2, several dry colonies, and 1 in alcohol, USNM 1016659, 1016659, 1112693.

TYPES AND TYPE LOCALITY: Holotype deposited at the NMNH (USNM 79966). Type locality: 25° 21′ 02″ N, 168° 09′ W (Gardner Pinnacles), 1,028 m.

REMARKS: These three records are the first subsequent to the original description and extend the known distribution substantially to the east of the type locality off Moloka'i. Table 3 serves to distinguish this species from congenerics in the Hawaiian Islands. In this regard *F. medialis* is distinctive in having pointed marginal scales, multipointed opercular scales, coenenchymal bosses, and a rather large number of outer lateral scales.

DISTRIBUTION: Northwestern Hawaiian Islands (Gardner Pinnacles), channel between Moloka'i and O'ahu, 395–1,028 m.

## Genus *Parastenella* Versluys, 1906

DIAGNOSIS: Colonies uniplanar to slightly bushy, dichotomously branched. Polyps arranged in whorls, pairs, or isolated, usually standing perpendicular to branch. Eight marginal scales, most of which are fluted, are offset from the 8 opercular scales. Body wall covered with 5–8 rows of scales, the adaxial side sometimes naked. Opercular scales keeled. Tentacular rods often present.

TYPE SPECIES: *Stenella doederleini* Wright & Studer, 1889, by subsequent designation (Bayer 1956:F222).

REMARKS: The genus has been most recently discussed by Cairns (2007*a*,*b*) and Cairns and Bayer (2009). Seven species are now considered to constitute the genus, which are keyed here.

DISTRIBUTION: Cosmopolitan except for eastern Atlantic and off continental Antarctica, 517–3,470 m.

KEY TO THE *Parastenella* SPECIES

1. Marginal scales of uniform size and flutes consistently present, forming a symmetrical rosette ..... 2
1′. One to 3 marginal scales on adaxial side of polyp reduced in size and lacking flute, forming an asymmetrical rosette..... 5

2. Body wall scales in 8 rows ..... 3
2′. Body wall scales in 5 or 6 rows ..... 4

3. Body wall and coenenchymal scales ridged; tentacular rods common..... ..... *pacifica* Cairns, 2007*b* (Oregon to British Colombia, 1,527–1,986 m)
3′. Body wall and coenenchymal scales not ridged; tentacular rods rare..... .....*atlantica* Cairns, 2007*a* (New England Seamounts, 1,984 m)

4. Abaxial submarginal body wall scales with flutes; marginal scale flutes narrow; 5 rows of body wall scales..... *spinosa* (Studer, 1894) (southern Indian Ocean, 567 m)
4′. Abaxial submarginal body wall scales lacking flutes; marginal scale flutes broad; 6 rows of body wall scales..... *bayeri* Cairns, n. sp. (Hawai'i, 517 m)

5. Marginal scale flutes broad; adaxial side of polyp naked ..... ..... *gymnogaster* Cairns, 2007*b* (Oregon to Alaska, 1,962–2773 m)
5′. Marginal scale flutes narrow (tubular); adaxial side of polyp covered with scales ..... 6

6. Marginal scale flutes quite narrow and long (up to 53% length of sclerite); polyp up to 2.2 mm tall; coenenchymal scales with bosses..... .....*doederleini* (Wright & Studer, 1889) (Japan, Indonesia, 732–3,427 m)
6′. Marginal scale flutes only moderately narrow, 38%–46% length of sclerite; polyps up to 3.3 mm; coenenchymal scales lack bosses ..... .....*ramosa* (Wright & Studer, 1889) (northeastern Pacific, 665–1,750 m)

*Parastenella bayeri* Cairns, n. sp.
Figures 1*F*, 12*B–E*, 13

*Parastenella* n. sp. Parrish and Baco, 2007:193 (listed).

TYPES AND TYPE LOCALITY: Holotype: a colony and 3 branches, *Pisces 5*-593 (specimen 15), USNM 1071249. Type locality: 19° 48′ 12″ N, 156° 08′ 02″ W (off Keāhole Point, Hawai'i), 517 m.

DESCRIPTION OF HOLOTYPE: Colony uniplanar, but with 2 overlapping flabella, the largest fragment 28 cm tall and 13 cm wide, having a broken base 2.9 mm in diameter. Branching irregularly dichotomous. Axis golden bronze, covered by white polyps and coenenchyme. Polyps up to 3.0 mm in height, slightly flared distally (1.5–1.7 mm diameter), standing perpendicular to branch. Polyps occur in pairs, whorls of 3–4, and occasionally isolated, the latter common on larger-diameter branches. About 4 whorls per cm; whorl diameter about 5 mm.

Eight fluted marginal scales of the same size (0.9–1.1 mm length) and shape form a symmetrical rosette when viewed from above. Flutes of marginal scales quite shallow and broad (Figures 12*D*, 13*B*), occupying entire width of marginal scale and 32%–37% of its length. Flutes do not occur on submarginal scales. Six submarginal scales surround upper perimeter of polyp: 2 broad (0.65–0.75 mm) abaxial scales, 2 slightly narrower lateral scales, and 2 smaller (0.4–0.45 mm) adaxial scales. Each submarginal is part of a row of 3 or 4 scales, the scales quickly reducing in size toward base of polyp. Body wall scales elliptical, with a concave upper surface that is smooth to mildly granular, and a smooth distal edge.

Opercular scales fairly uniform in size (1.0–1.1 mm long), having a deeply longitudinally creased outer surface that corresponds

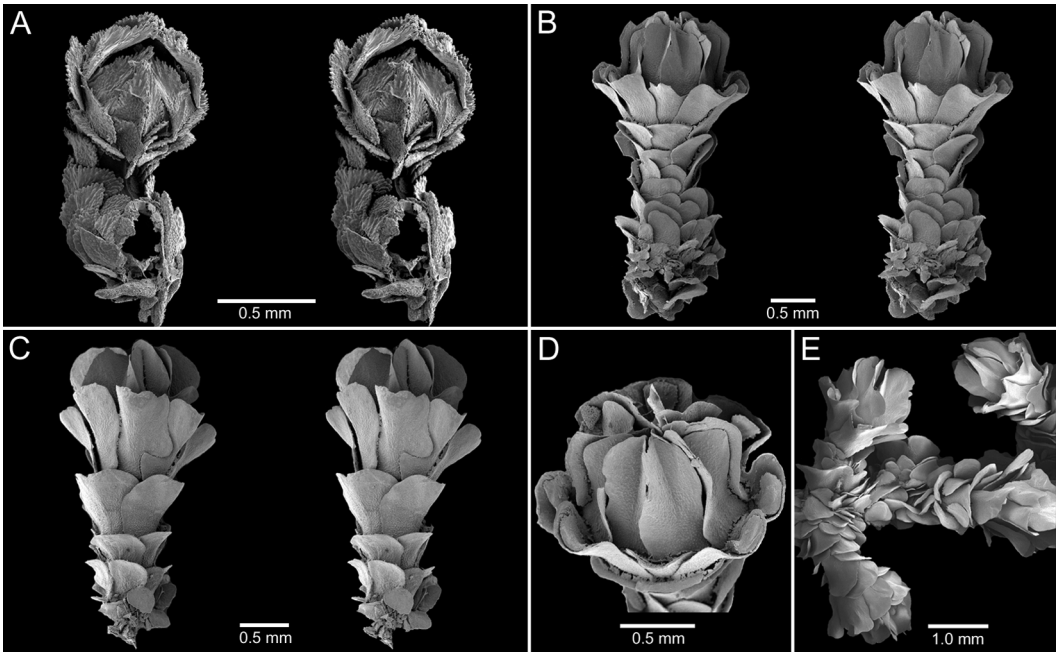


FIGURE 12. *A*, Polyps of *Callogorgia formosa*, USNM 60292; *B–E*, polyps of *Parastenella bayeri*, n. sp., USNM 1071249 (holotype); *A–C* are stereo views: *A*, adaxial view of a polyp; *B*, adaxial view of a polyp; *C*, abaxial view of a polyp; *D*, oblique opercular view of a polyp, showing some of the nematocyst pads on inner sides of marginal scales; *E*, a whorl of polyps.

to a sharply keeled inner surface; opercular tips sharply pointed or blunt. Abaxial and adaxial operculars symmetrical, whereas lateral operculars asymmetrical, having a lobe on their adaxial side. Abaxial scales sometimes broadly notched on both sides near the base (Figure 13*A*), as well as sometimes bearing a deep slit on their distal edge just off their midline. L:W of abaxial opercular scales 1.1–1.3; of lateral opercular scales, 1.3–2.3; and of adaxial operculars, 1.8–2.4.

Coenenchymal scales similar to proximal body wall scales in size (0.4–0.5 mm in diameter) and shape: elliptical, concave, smooth to mildly granular, and not ridged. Tentacular (pinnular) rods not noted.

COMPARISONS: *Parastenella bayeri* is remarkably similar to *P. atlantica* Cairns, 2007*a* (see Cairns 2007*b*: table 2), differing only in having 6, not 8, rows of body wall scales and in completely lacking tentacular rods. The original description of *P. atlantica* did not allow for polyp whorls, but Cairns (2007*b*) amended that observation to include whorls of 2–4 polyps, consistent with *P. bayeri*. Given the wide geographic and bathymetric separation of *P. atlantica* (New England Seamounts, 1,984 m) from *P. bayeri* and the fairly trivial morphological distinctions between them, *P. bayeri* eventually might be found to be a geographic subspecies of *P. atlantica*.

REMARKS: On the inner distal region of each marginal scale, occupying the concave fluted portion of the scale, is a rectangular pad measuring about 0.3 mm wide and 0.1 mm deep (Figure 12*D*), consisting of a dense concentration of closely packed nematocysts. The nematocysts are about 19 μm long and 1.8–1.9 μm in diameter, and oriented perpendicular to the scale; approximately 1,000 constitute each pad (Figure 13*D*, *F*). These pads are ideally located to defend the polyp because they would surround the operculum and polyp when the polyp is expanded. Similar pads have been illustrated for *P. gymnogaster* (Cairns 2007*b:* fig. 6*C*) and may be a common character for this genus.

ETYMOLOGY: Named in honor of Freder-

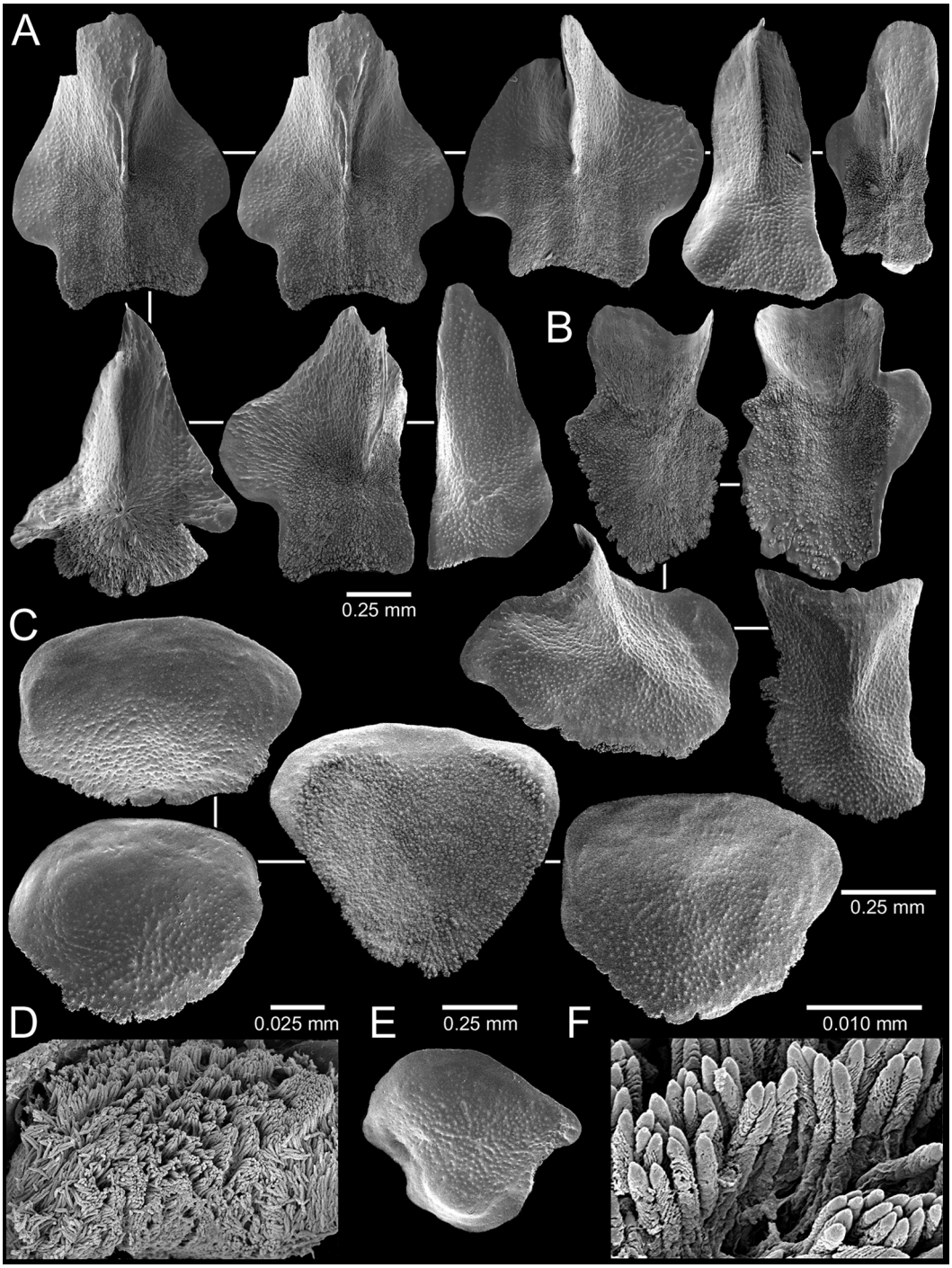


FIGURE 13. Sclerites of *Parastenella bayeri*, n. sp., USNM 1071249 (holotype): *A*, opercular sclerites, upper left being a stereo pair; *B*, fluted marginal sclerites; *C*, body wall sclerites; *D*, *F*, nematocysts from marginal scale pads; *E*, coenenchymal sclerite.

ick M. Bayer, who has described the largest number of Hawaiian primnoid species (Table 1) (see Cairns 2009*b*).

DISTRIBUTION: Known only from the type locality.

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**Appendix**

Station Data

| Vessel/Cruise | N Latitude | W Longitude | Depth (m) | Date |
|---|---|---|---|---|
| USFWS *Albatross* (*Alb*) | | | | |
| 3973 | 23° 47′ 10″ | 166° 24′ 55″ | 722–726 | 29 May 1902 |
| HURL | | | | |
| 82-103 | 21° 18′ | 157° 33.5′ | 366 | 14 June 1982 |
| *Pisces 4* | | | | |
| 45 | 20° 29′ 10″ | 156° 39′ 54″ | 299 | 3 Sept. 2002 |
| *Pisces 5* | | | | |
| 527 | 25° 48′ 43″ | 173° 30′ 27″ | 608–1,209 | 10 Oct. 2003 |
| 528 | 25° 49′ 08″ | 173° 27′ 12″ | 472 | 11 Oct. 2003 |
| 535 | 25° 30′ 32″ | 169° 23′ 20″ | 305 | 21 Oct. 2003 |
| 543 | 23° 13′ 55″ | 163° 31′ 07″ | 1,278–1,723 | 1 Nov. 2003 |
| 582 | 21° 18′ 10″ | 157° 32′ 07″ | 388–440 | 2 Oct. 2004 |
| 583 | 21° 19′ 13″ | 157° 32′ 52″ | 419–426 | 3 Oct. 2004 |
| 587 | 18° 43′ 59″ | 158° 15′ 44″ | 389 | 8 Oct. 2004 |
| 589 | 18° 43′ 05″ | 158° 15′ 41″ | 388 | 10 Oct. 2004 |
| 590 | 18° 44′ 03″ | 158° 15′ 42″ | 447 | 11 Oct. 2004 |
| 593 | 19° 48′ 12″ | 156° 08′ 02″ | 517–750 | 15 Oct. 2004 |
| 668 | 21° 12′ 37″ | 156° 47′ 31″ | 466 | 2 Sept. 2006 |
| 670 | 31° 11′ 47″ | 156° 47′ 47″ | 680 | 4 Sept. 2006 |
| SANGO (University of Hawai‘i, *TC*) | | | | |
| 3-1a | 21° 19.5′ | 157° 32.4′ | 415–465 | 10 Aug. 1970 |
| 3-1b | 21° 18.46′ | 157° 30.6′ | 215–395 | 12 Aug. 1970 |
| 3-2 | 21° 17.4′ | 157° 32.3′ | 340–465 | 10 Aug. 1970 |
| 3-7 | 21° 18′ 08″ | 157° 32′ 43″ | 215–395 | 12 Aug. 1970 |
| 3-8 | 21° 17.9′ | 157° 32′ | 355–385 | 12 Aug. 1970 |
| 4-1 | 21°17′ 54″ | 157° 32′ 18″ | 326 | 29 Sept. 1970 |
| 4-8 | Off Makapu‘u Point, O‘ahu | | ? | 12 Oct. 1970 |
| 9-2 | 21° 15.4′ | 158° 07.9′ | 106–564 | 30 Apr. 1971 |
| 10-2 | 21° 19′ | 157° 33′ 06″ | 435–481 | 17 June 1971 |
| 13-3 | 24° 00′ 54″ | 166° 43′ 27″ | 384–432 | 23 Aug. 1971 |
| 14-1 | 21° 18.0′ | 156° 32.9′ | 362 | 18 Jan. 1972 |
| 14-2 | 21° 18.82′ | 157° 32.2′ | 344–454 | 18 Jan. 1972 |
| SANGO (Midway cruise) | | | | |
| 17 | 24° 21.92′ | 167° 57.96′ | 870–922 | 31 July 1972 |
| 20 | 24° 07′ 40″ | 160° 41′ 40″ | 745–932 | 1 Aug. 1972 |
| 25 | 23° 14.78′ | 162° 36.25′ | 360–385 | 3 Aug. 1972 |
| *Star II* (Maui Divers Jewelry Co. submersible) | | | | |
| 1 | 21° 18′ | 157° 32′ | 366–372 | 27 Jan. 1978 |
| 2 | 21° 18′ | 157° 32′ | 367 | 1 Feb. 1978 |
| *Townsend Cromwell* (*TC*) | | | | |
| 35-23 | 21° 15.36′ | 156° 25′ 30″ | ? | 15 Apr. 1968 |
| 59-20 | 21° 07′ 00″ | 156° 12′ 42″ | 786 | 16 July 1972 |
| 76-06-73-15 | 23° 33′ | 164° 54′ | 419–420 | 21 Oct. 1976 |
| 78-5 | Near Middle Bank | | ? | 11 Jan. 1978 |